PERIODICAL
5(37)

5(37)

BULLETINS
OF
MARINE ECOLOGY
(FORMERLY HULL BULLETINS OF MARINE ECOLOGY)

Edited by: A. C. HARDY, D.Sc., F.R.S.,
C. E. LUCAS, C.M.G., D.Sc., and K. M. RAE, O.B.E., B.Sc.

No. 37, Vol. V. Pp. 211—246

JUNE, 1957 *Price* 12*s.*

CONTINUOUS PLANKTON RECORDS:
THE DISTRIBUTION OF *CALANUS FINMARCHICUS* (GUNN.) IN THE NORTH SEA AND NORTH-EASTERN ATLANTIC, 194[illegible]53

BY

The late C. B. REES, D.Sc.

SEP 1957
LIBRARY
FOFI
FISH & WILDLIFE
SERVICE

PUBLISHED BY
THE SCOTTISH MARINE BIOLOGICAL ASSOCIATION
AT THE OCEANOGRAPHIC LABORATORY
EDINBURGH

[*Bulletins of Marine Ecology, Vol. V, No.* 37, *pp.* 211–246, *Plates I–IV, June* 1957.]

CONTINUOUS PLANKTON RECORDS: THE DISTRIBUTION OF *CALANUS FINMARCHICUS* (GUNN.) IN THE NORTH SEA AND NORTH-EASTERN ATLANTIC, 1946–1953

BY

The late C. B. REES, D.Sc.

[While preparing this paper for publication Colin Rees was taken seriously ill and died before seeing the first proof; had he lived, he might have polished and revised his draft. While we have made a few obvious corrections to the text, we have felt it desirable to alter it as little as possible for fear of unintentionally changing his meaning.—*The Editors.*]

CONTENTS.

	PAGE
Introduction and Methods	212
The Distribution of *Calanus*	215
Spatial Distribution of *finmarchicus* and *helgolandicus*	218
North Sea	218
Atlantic	220
Ratios of Stage V to adults	224
Seasonal Distribution of *Calanus*, *finmarchicus* and *helgolandicus*	225
North Sea	225
Coastal Atlantic	232
Oceanic Atlantic	234
Yearly Variations in Numbers	234
North Sea	235
Coastal Atlantic	236
Oceanic Atlantic	236
Discussion	236
Life histories	236
Water movements	240
The distribution in the Atlantic	243
Summary	244
References	245

Introduction and Methods.

In 1938 and 1939 the plankton recorder survey extended over most of the North Sea and the data referring to *Calanus finmarchicus* have been dealt with in some detail (Rees, 1949). We can now consider the results of the post-war survey over a period of eight years, from 1946 to 1953.

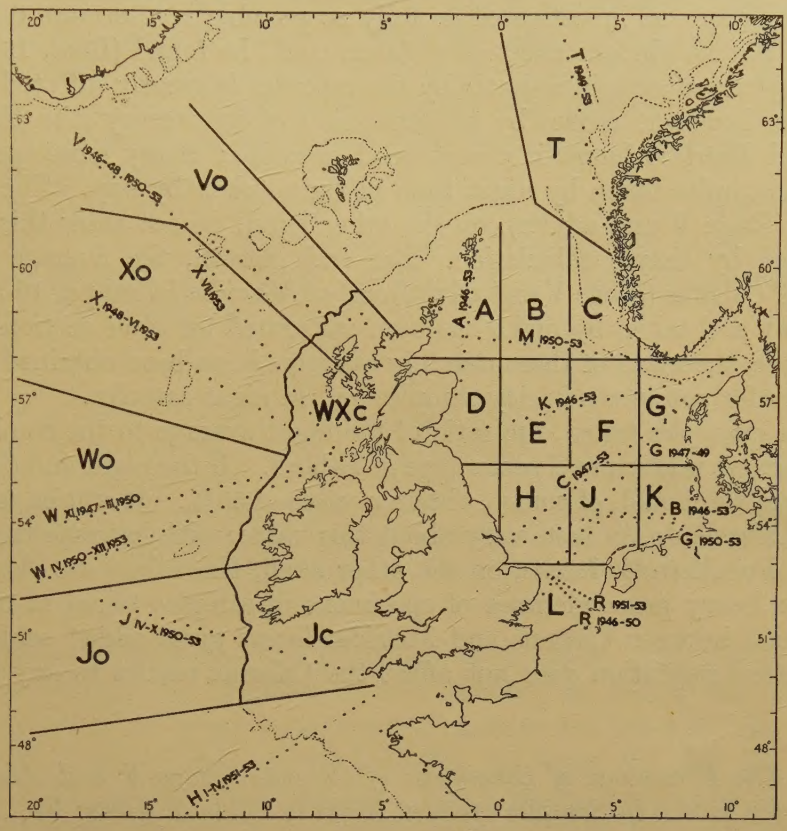
As in the earlier report, the two forms which are distinguished correspond to the *Calanus finmarchicus* and *C. helgolandicus* described by Sars (1903). It is still considered that these forms, though distinct, should not be ranked as species but should be regarded as forms of a single species, *C. finmarchicus* (Gunn.). The two forms are referred to as *finmarchicus* and *helgolandicus*, as in the previous report, the generic name Calanus being used for the undifferentiated specimens. This view on the status of the two forms has been somewhat strengthened by the results of experiments of Marshall and Orr (1952). They found that Calanus eggs usually fell into two size groups, the larger laid by *helgolandicus*, the smaller by *finmarchicus*, but occasionally eggs of intermediate size were seen. The occurrence of these intermediate eggs agrees with the view that the two forms can and do interbreed.

The scope of the post-war survey, the method of plankton analysis employed and the distribution of the records in each month have been described by Rae (1952, 1953). The amount of detail now available within the North Sea is much less than in 1938–39. Firstly, some recorder routes in the North Sea have not been resumed. Secondly, only alternate 10-mile samples have been analysed in records taken since the war. Thirdly, the analysis of the plankton has been less detailed. It is now the practice to estimate the number of Calanus in two groups ; first, all stages from copepodid Stage I upwards, and secondly, Stage V and adults combined. They are only estimated approximately into broad arithmetic categories. For example, samples estimated as containing 126 to 250 Calanus Stage V and adults are all included in a single category and each is regarded as containing 160 Calanus (Rae, 1952, p. 147). In contrast, copepodid Stages I—III combined, Stage IV, Stage V, females and males were each estimated more exactly in the 1938–39 material. The approximate numbers of Stages I–IV in post-war samples can be obtained by substracting the estimated number of late stages from that of all stages. In the following account the Stages I–VI will be referred to as total Calanus, Stages I–IV as young Calanus and Stage V and adults as late Calanus.

The extension of the recorder survey over a wider area has more than compensated for the reduced sampling in the North Sea. The scope of the survey since 1946 is illustrated in Text-fig. 1. The routes are designated by letters and the periods over which records have been taken on each route are given.

Because of the quantity of the information (data for eight years in the North Sea and six in the Atlantic) the results can be treated only very broadly. However, particular attention has been given to the distribution of the two forms *finmarchicus* and *helgolandicus*. In the somewhat crushed recorder material a simple diagnostic,

such as forehead shape, is not entirely satisfactory for the differentiation of the forms, and in each specimen the arrangement of teeth on the basipod of the 5th legs of Stage V and females must be checked (Rees, 1949). This is a slow process and consequently only a small portion of the material has been separated. Small sub-samples have been examined and the populations of the two forms estimated where so required, proportionately and by interpolation. The sub-sample con-



TEXT-FIG. 1.—Chart showing the recorder routes normally in use from 1946 to 1953. The routes are designated by the smaller letters and the periods over which the routes were operated are given. The dots mark the approximate positions of the 10-mile samples which were analysed. The heavy lines mark off areas designated by the larger letters. Samples within each area have been grouped to provide estimates of average number of specimens per 10-mile sample. See also Text-fig. 9.

sisted, irrespective of sample size, of a maximum of twenty specimens, ten Stage V and ten females, but when one of the two stages was not readily available in a sample fewer than ten of it were differentiated. Thus in one sub-sample ten Stage V and two females may have been separated, in another four Stage V and ten females. By keeping the sub-samples small it has been possible to take a

large number, covering the whole eight years and, with the exception of the Norwegian Sea samples (T route) in which it is obvious that *finmarchicus* is overwhelmingly predominant, the whole region of the survey. Altogether, 11,000 specimens have been differentiated.

It must again be emphasized that the recorder is towed at a depth of 10 m. and that all the information available refers to that single depth.

The possible effect of diurnal vertical migration upon numbers obtained by night and by day was investigated as fully as possible in the more detailed data for 1938–39 but no obvious effect on Calanus could be found (Rees, 1949, p. 218). That the capture of certain animals by the recorder is greatly affected by diurnal migration is, however, shown by the extension of the survey into the Atlantic. The copepod *Metridia lucens* is a very good example; many more specimens are obtained in samples taken by night than in those taken by day. The late stages of Calanus (Stage V and adults), on the other hand, do not show this, as can be demonstrated by simple calculation. For each month, the average number of specimens of Calanus (Stage V and adults) and of *Metridia lucens* per 10-mile sample taken by day and taken by night has been calculated for some sections of routes. For each year, the mean of these monthly averages,[1] has been obtained to give the overall mean for specimens in day samples and in night samples.

For the examples taken, the ratio of the night average to the combined night and day averages is given as a percentage in Table I. If the night and day averages were identical we should, of course, obtain a value of 50%. It will be seen that the values for Calanus do, in fact, vary about this value, with extreme limits of 35% and 66%. For *Metridia lucens*, on the other hand, the values are closer to 90%, showing the heavy preponderance of specimens in samples taken at night. This sharp contrast between Calanus and *Metridia lucens* gives added confidence that diurnal vertical migration does not affect the Calanus results to any appreciable extent.

TABLE I.—*The Percentage of Specimens of Calanus (Stage V and Adults) and of* Metridia lucens *in Samples taken at Night in Atlantic Areas: Vo, Xo and Jc (Text-fig.* 1).

	Calanus.			Metridia.		
	Vo.	Xo.	Jc.	Vo.	Xo.	Jc.
1948	46	42	—	95	95	—
1949	—	47	—	—	78	—
1950	—	40	61	—	88	98
1951	66	35	59	78	78	97
1952	46	60	48	95	97	93
1953	55	65	48	88	90	96

[1] By taking the mean of the monthly averages one avoids bias due to the fact that the proportion of day samples to night samples varies through the year, high in summer, low in winter.

The Distribution of Calanus.

The data concerning Calanus, obtained during the 1938–39 survey, were summarized by sub-dividing the North Sea into arbitrary areas and calculating the average number of individuals per 10-mile sample within each area (Rees, 1949). This method is again used. The areas, or the groups of samples which are taken together, are shown in Text-fig. 1. There are insufficient post-war results from the North Sea areas B, C and K, but there are now extensive data from outside the North Sea. These samples have been grouped into Jo, Wo, Xo, Vo (o stands for " oceanic ", samples taken outside the 100-fm. contour), Jc, WXc (c stands for " coastal ", samples taken inside the 100-fm. contour) and T, which is taken as a single group.

An average has been calculated for total Calanus and for late Calanus per 10-mile sample within each area in each month and also an average per sample for the whole of each year. These averages are not given here although they are incorporated in certain estimates.

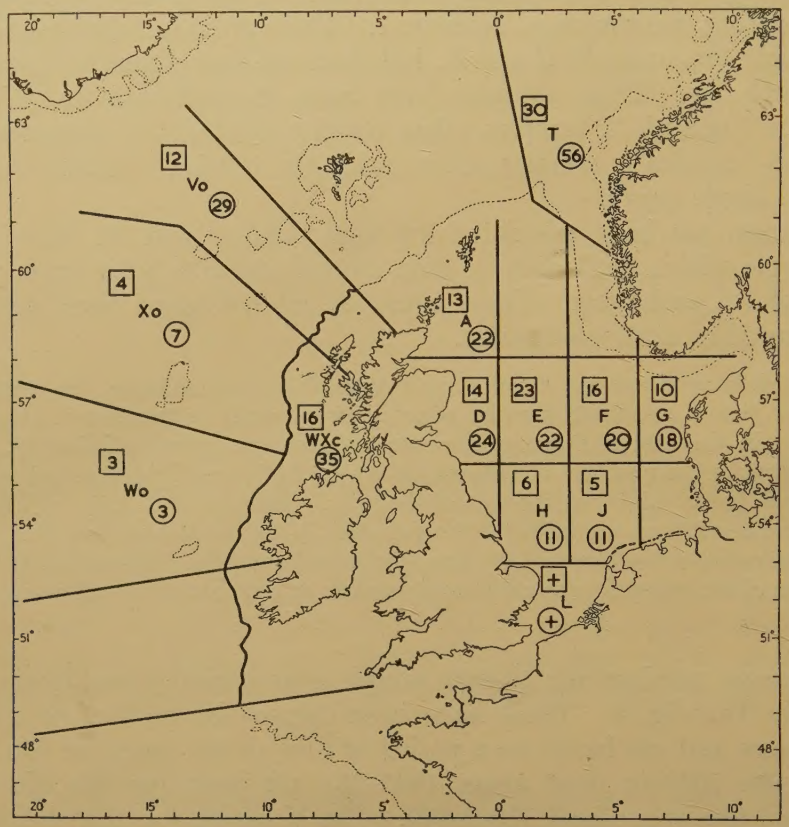
For several copepod species, which have long periods of abundance, the average number per sample per year is a satisfactory way of comparing overall fluctuations in abundance from year to year. In the case of Calanus, however, this method is less satisfactory. There is a general tendency for the numbers of Calanus to be very high over a short period and to change rapidly to much lower values for the rest of the year. The period of high, changing numbers has a considerable effect on the value for the year and, in any particular case, it is by no means certain that the recorder was towed at the time of maximal numbers. This difficulty is minimized when the mean of the values for several years is used as an estimate of overall population density in an area.

The average numbers per 10-mile sample over several years within each area are shown in Text-fig. 2. These have been derived by taking the mean of the yearly averages and are based on a period of nine or ten years for the North Sea areas (1938–39, 1946 in most areas, 1947–53), six years for Wo, Xo and WXc (1948–53) and five years for T (1949–53). The V record was towed so irregularly that the average numbers for Vo have been estimated from the monthly averages ; the resultant estimates are less satisfactory than those for other areas but are doubtless of the correct order. The J record was towed usually only from April to September so that values for areas Jo and Jc are not given here.

Over the limited period 1938–39 total Calanus was far more abundant in the north-west North Sea, area A, than in the other areas of the North Sea ; the average population density in area F was less than one-third that in A (Rees, 1949). This was not typical over a longer period for, as Text-fig. 2 shows, the population density in area A was no more than moderate and substantially less than in the central North Sea (areas E and F). The population in the Skagerrak (G) was comparatively smaller than the 1938–39 results suggest.

The greatest interest of Text-fig. 2 lies in the comparison which may be made between the North Sea and the areas outside it. The average numbers both of

total Calanus and late Calanus were very low in the oceanic Atlantic samples of Wo and Xo, and increased rapidly going northwards to Vo, and finally to the greatest value of all in the Norwegian Sea, T. In the coastal Atlantic area WXc, the average for total Calanus was greater than the average for the North Sea as a whole and for late Calanus much above that of the North Sea average.



TEXT-FIG. 2.—Chart showing the average number of specimens, over many years, per 10-mile sample in the various areas of the survey. The average numbers of Calanus, all stages from copepodid Stage I upwards, are enclosed in squares and of Stage V and adults combined, in circles. The numbers for all stages, in the squares, have been divided by ten.

It can be said, from a comparison of monthly averages, that the overall population density in the Shelf area south of Ireland (Jc), while greater than in Xo, was only about half that north of Ireland (WXc). As might be expected, the population density in Jo was very low, just about equal to that in Wo.

Text-fig. 3 also illustrates the distribution of late Calanus; in each chart the dots show the positions of samples containing more than certain numbers of specimens. The over-50 category is shown only for the Atlantic. There has not been, unfortunately, equality of sampling over the whole area. Only samples taken

over six years are included for the North Sea so as to correspond with the period covered by the W and X routes; the T route has been sampled for five years and the J route for four (for routes see Text-fig. 1). On the V route there have been only about half as many records as on each of the W and X routes and its coastal section has been very poorly sampled.

TEXT-FIG. 3.—Charts showing the positions of 10-mile samples containing over 50, over 125, over 250 and over 500 *late* Calanus (Stage V and adult). Only the results from the Atlantic routes are included for the over-50 category.

Text-fig. 3 illustrates clearly the increasing density of Calanus going northwards and the scarcity in oceanic water west of Ireland. Although, in general, the overall numbers of late Calanus were lower in Jc than in WXc, samples containing more than 125 and 50 specimens were comparatively numerous. It can be seen in Table II that the percentage of all samples, taken between April and September, which contained more than 50 Calanus is slightly higher in Jc than along the Leith–Skagerrak (K) line and not far short of the percentage north of Ireland (WXc). However, as the population densities greater than 125 are considered, there are fewer and fewer examples to be found south of Ireland.

TABLE II.—*Percentages of Samples containing Large Numbers of the Forms,* finmarchicus *and* helgolandicus *South* (Jc) *and North of Ireland* (*WXc*), *in the Norwegian Sea* (*T*) *and along the Leith–Skagerrak* (*K*) *and Hull–Copenhagen* (*C*) *Routes. Only Samples taken from April to September,* 1948 *onwards are included. For Details of Areas and Routes see Text-fig.* 1.

	Jc.	WXc.	T.	K.	C.
Total number of 10-mile samples . .	251	385	380	753	633
% of samples with 50 Calanus . .	25	29	44	23	7
% ,, ,, ,, 125 Calanus . .	8	12	31	8	2
% ,, ,, ,, 50 *finmarchicus* .	3	18	44	19	4
% ,, ,, ,, 50 *helgolandicus* .	21	10	0	4	3

THE DISTRIBUTION OF *FINMARCHICUS* AND *HELGOLANDICUS*.

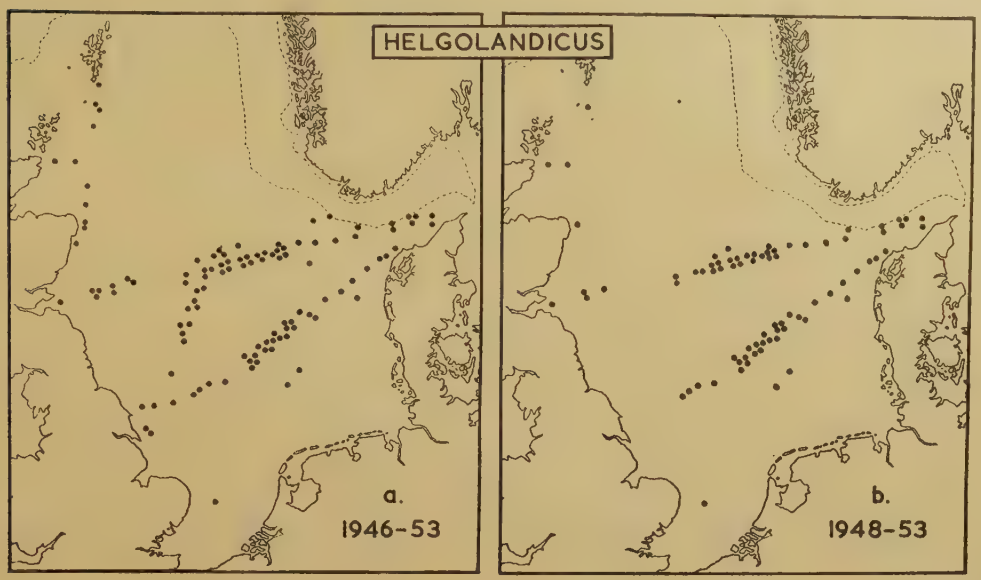
The distribution of the two forms *finmarchicus* and *helgolandicus* in the North Sea was studied in the 1938–39 material. It was found that *finmarchicus* was a northern form and much the commoner of the two, while *helgolandicus* was found chiefly in the centre of the North Sea and reached its greatest population density later in the year than *finmarchicus* (Rees, 1949).

Russell (1951) found *helgolandicus* predominant in samples taken off Plymouth in 1926, 1930 and 1931. In a series of samples taken from April to September 1926, *finmarchicus* occurred only between April to June and the maximum in any one sample was 10%.

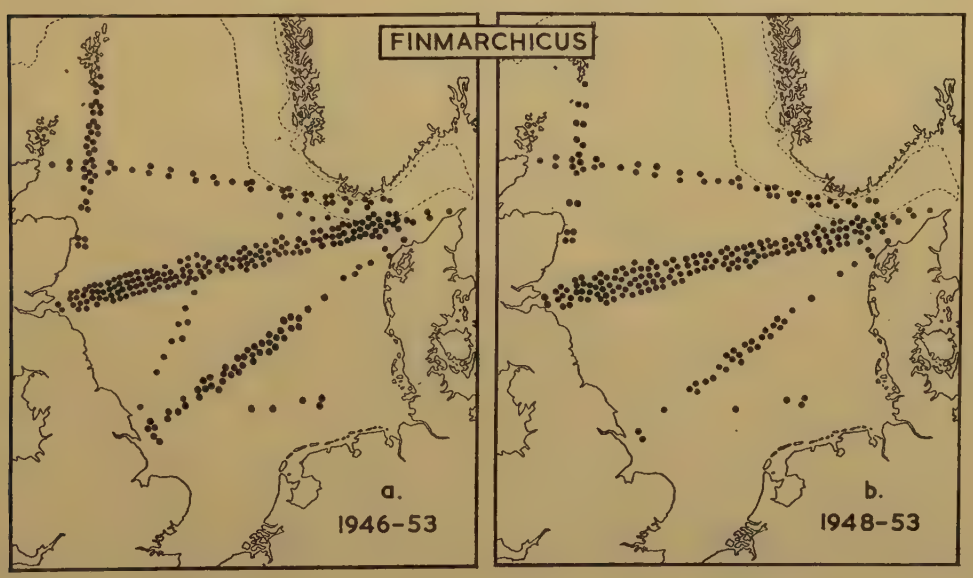
Marshall and Orr (1955, p. 6) found that the percentage of *helgolandicus* was high at times in the Clyde Sea area. In the autumn of 1951 the percentage of *helgolandicus* was 32% and higher still in the autumns of 1952 and 1953.

North Sea.

The numbers of *finmarchicus* and *helgolandicus* in all 10-mile samples from the North Sea containing more than 25 late Calanus have been estimated, and are shown in the charts in Plates I to IV. It can be seen that concentrations of *helgolandicus* were quite common, more so in some years than in others. Exceptionally



TEXT-FIG. 4.—Charts showing the positions of all 10-mile samples found to contain more than 50 Stage V and adults of *helgolandicus* in the North Sea from (*a*) 1946 to 1953, (*b*) 1948 to 1953.



TEXT-FIG. 5.—Charts showing the position of all 10-mile samples found to contain more than 50 Stage V and adults of *finmarchicus* in the North Sea from (*a*) 1946 to 1953, (*b*) 1948 to 1953.

rich concentrations sometimes occurred in the north-west (1946) but, in general, they were found most consistently along the centre of the Leith–Copenhagen line (Great Fisher Bank) and the centre of the Hull–Copenhagen line (eastern Dogger Bank). The distributions are summarized in Text-fig. 4,[1] all samples containing more than 50 *helgolandicus* being indicated by a dot. A not dissimilar chart has been given for 1938–39 (Rees, 1949, Text-fig. 4) but this included only Stage V whereas Text-fig. 4 gives a summation of both Stage V and adults. Observations are most clustered in an area which includes the Great Fisher Bank and the eastern half of the Dogger Bank. This tendency is more apparent when the samples of 1946 and 1947 are excluded (Text-fig. 4*b*).

The comparable distribution of *finmarchicus* is shown in Text-fig. 5. It is clear that *finmarchicus* was much more common than *helgolandicus*. An interesting feature of the chart for 1948–53 (Text-fig. 5b) is that the main concentrations of *finmarchicus* in the southern half of the North Sea occurred not between the Humber and Dogger Bank but well to the east of this region. In this aspect the two forms resemble each other (Text-fig. 4).

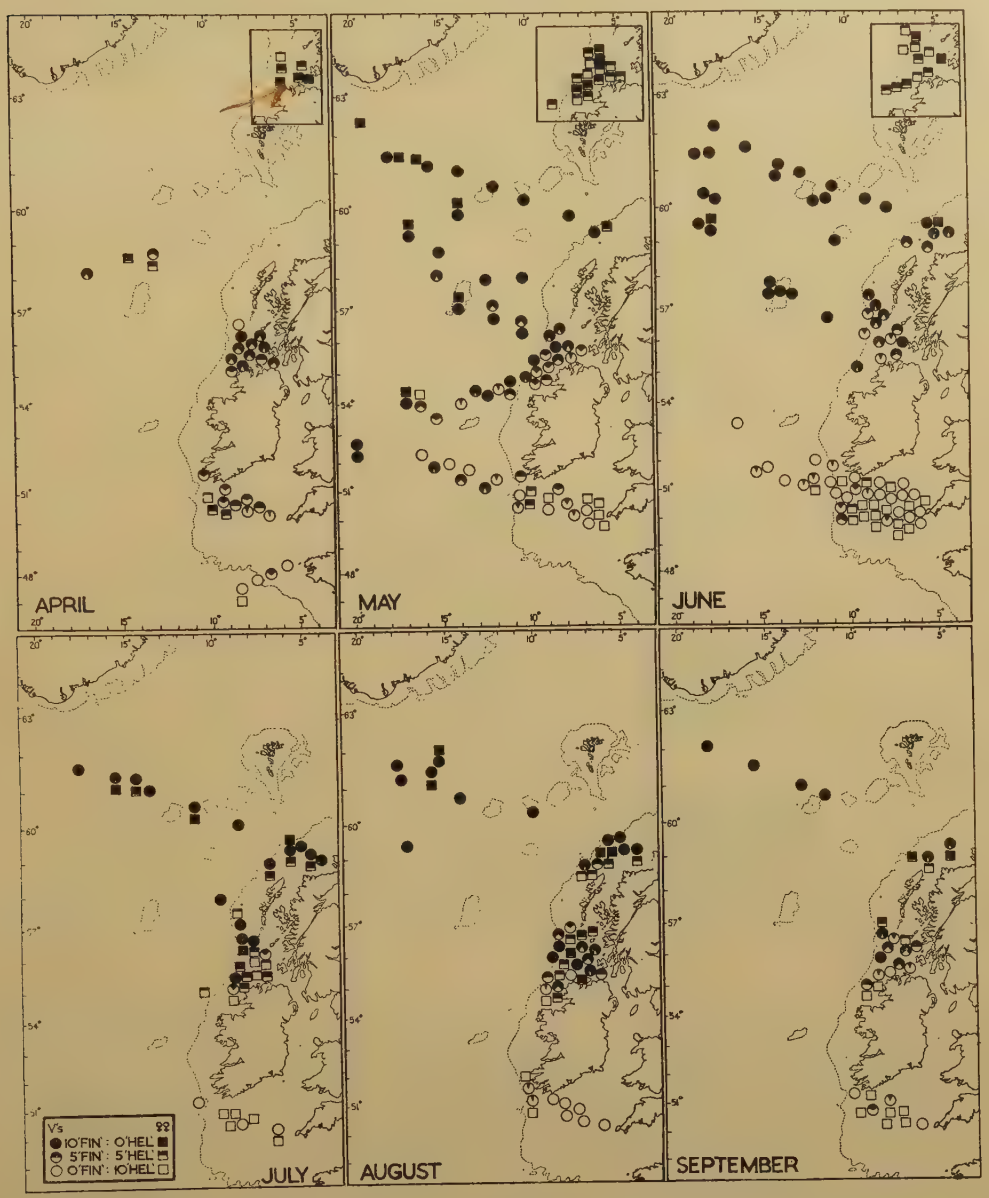
Atlantic.

Rees (1949, Text-fig. 3) showed the proportions of *finmarchicus* and *helgolandicus* in the populations of Stage V over the North Sea during several months of 1938–39 on charts by means of circles, sections being blacked-in to represent the proportion of *finmarchicus*. A similar method is used for the Atlantic in Text-fig. 6. In these charts the proportions of the two forms in the populations of females are also shown, in this case by squares. To avoid overcrowding the square symbols for the coastal waters north of Ireland from April to June are given in displaced charts; many of the circular symbols are, of course, also slightly displaced to avoid overlapping. The samples differentiated in each month from April to September are shown, irrespective of year, in single charts.

There were very few samples in which any *helgolandicus* were observed in the oceanic waters north of latitude 57°N. (Rockall Bank), and nearly all of these occurred in April. It was only in May and June that samples containing appreciable numbers of late Calanus were obtained in the oceanic water south of the Rockall Bank. Some of these samples in May contained *helgolandicus* only, others *finmarchicus* only, the general impression being that the Calanus were about equally divided between the two forms. In June, *helgolandicus* was markedly predominant but samples came from a more restricted area.

Both forms were present in the coastal waters south of Ireland in April and May but *helgolandicus* was more common than *finmarchicus*. From June onwards the proportion of *finmarchicus* became, and remained, very small. There was no marked seasonal change in the proportions in the coastal waters north of Ireland. *Finmarchicus* was predominant north of Scotland but, again, some samples contained an appreciable proportion of *helgolandicus*.

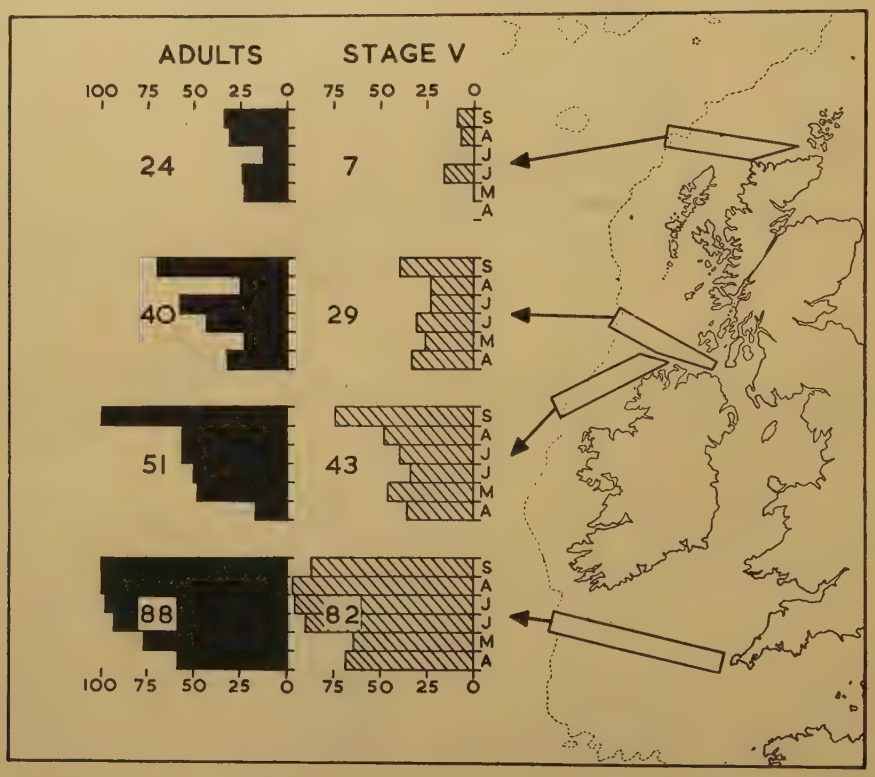
[1] It should be noted that the Pentland Firth–Skagerrak route was sampled only occasionally.



TEXT-FIG. 6.—Monthly charts showing the proportions of *finmarchicus* and *helgolandicus* in samples of Stage V (circles) and adult females (squares) from the Atlantic. The black and white portions of the symbols show the proportions of *finmarchicus* and *helgolandicus* respectively. The symbols for females north of Ireland have been displaced in the charts for April to June.

All samples, including some not shown in Text-fig. 6 are combined in Text-fig. 7. The histograms show, all years being combined for each month, the percentage of *helgolandicus* in the Stage V and females examined in four coastal Atlantic areas. The numbers adjacent to the histograms are the overall percentages in each area for the whole period.

Text-fig. 7 confirms the impression, gained from Text-fig. 6, that the proportion of *helgolandicus* in the population decreased northwards. It is noticeable that the percentage of *helgolandicus* north of Ireland was quite high, 40–50% in Wc



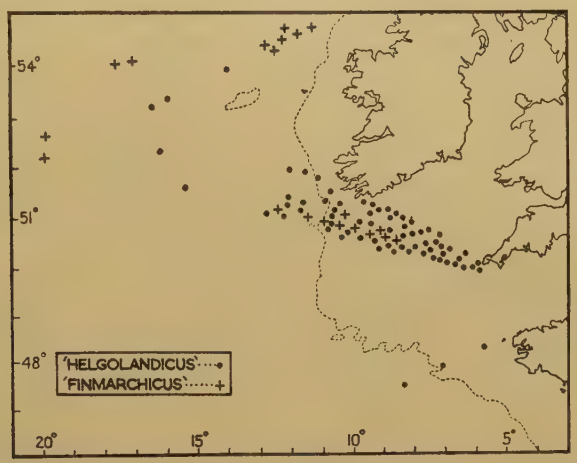
Text-fig. 7.—Histograms giving the percentages of *helgolandicus* in all adult females (black histograms) and in all Stage V (hatched histograms) Calanus differentiated in each month, all years combined, in four Atlantic coastal areas. The numbers adjacent to each set of histograms gives the overall percentages, all months and years combined.

and 30–40% in Xc. In the monthly values there is a tendency towards an increasing proportion of *helgolandicus* from April to September in Jc and Wc but there is no distinct trend in Xc and Vc.

As seen in Text-fig. 6, the oceanic region north of the Rockall Bank contained *finmarchicus* in overwhelming predominance, while south of the Rockall the population was mixed. Text-fig. 8 shows the distributions of samples containing more than 50 *finmarchicus* and of samples containing more than 50 *helgolandicus* in the oceanic

region south of lat. 55°N. and in the coastal water south of Ireland. It is noticeable that rich *finmarchicus* samples were found only in the western half of the section of the route from Land's End to the 100-fm. contour.

Whilst it is clear from Text-fig. 6 and 7 that *helgolandicus* was much commoner than *finmarchicus* south of Ireland and rather less common than *finmarchicus* north of Ireland, the values do not reveal whether *helgolandicus* was, in fact, numerically more abundant in one place than in the other. A very approximate estimate may be made by dividing the overall average numbers of late Calanus per month into the two forms according to the proportions which are shown in Text-fig. 7. When this is done the population ratio between south of Ireland and north of Ireland is estimated at 3 : 2 for *helgolandicus* and 1 : 6 for *finmarchicus*. Another way of estimating the relative population densities is to determine the proportion of all



TEXT-FIG. 8.—Chart showing the positions of all 10-mile samples containing over 50 Stage V and adults of *helgolandicus* or of *finmarchicus* in the south-western part of the recorder survey.

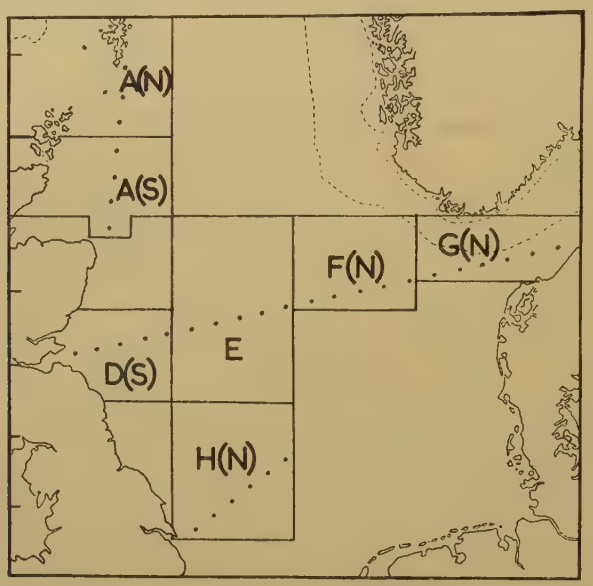
samples taken (April to September) which contained large numbers of *helgolandicus* and *finmarchicus*. The percentages obtained are given in Table II. These values agree very well with the ratios since samples containing large numbers of *helgolandicus* were found twice as frequently south of Ireland as in the north ; *finmarchicus* occurred in large numbers six times more frequently in the north as in the south.

An indication of the relative population densities of the two forms in the Atlantic and North Sea can also be gained from Table II. Text-fig. 2 shows that the average number of late Calanus per sample was substantially higher north of Ireland (WXc) than generally in the North Sea. This is confirmed in Table II by the percentages of samples containing large numbers of Calanus in WXc and along the Leith-Skagerrak (K) route which samples areas D, E, F and G. However, the percentage containing large numbers of *finmarchicus* was slightly higher

along the K route than in XCc ; the percentage of *helgolandicus* was, on the other hand, markedly higher in WXc. It appears, in fact, that the late Calanus population was richer in WXc than in the central North Sea because of the greater quantity of *helgolandicus* there. The percentage of *helgolandicus* on the Hull–Copenhagen (C) route was even lower than on the K route.

Ratios of Stage V to adults.

In the 1938–39 material it was estimated that 80% of the late *finmarchicus* (Stage V and adults combined) consisted of Stage V whereas only 44% of late *helgolandicus* were Stage V (Rees, 1949, p. 233). During 1946 to 1953 Stage V made up 78% of all the late *finmarchicus*



TEXT-FIG. 9.—Chart showing the sub-divisions of the North Sea used for a consideration of life history. These are the sub-divisions used for Text-fig. 10.

which were differentiated in the North Sea and 47% of all late *helgolandicus;* these values correspond closely to those of 1938–39.

Similar estimates have been made for the coastal areas north and south of Ireland. Since differentiation of forms was limited to the period April to September, a comparable estimate for only this period has been obtained for the North Sea. The percentages of Stage V in late *finmarchicus* and late *helgolandicus* are :

	Finmarchicus.	*Helgolandicus.*
North Sea	76	44
North Ireland	58	47
South Ireland	—	54

To explain this and other differences between *finmarchicus* and *helgolandicus* in the North Sea, the hypothesis was advanced that in summer the Stage V *finmarchicus* failed to moult successfully into adults because the temperature was too high at the time (Rees, 1949, p. 258).

As far as this particular feature is concerned some simple explanation might have been adequate, such as a differential depth distribution of stages and forms, or a natural difference in longevity. However, the contrast between the ratios is much less evident north of Ireland and this so tends to dispose of the simpler explanations.

Seasonal Distribution of Calanus, *finmarchicus* and *helgolandicus*

The seasonal distribution is primarily dependent on two factors. The first is the history of individual populations, involving reproduction, mortality and vertical migration relative to the 10 m. level sampled. The second is that of the transport of populations through water movements. These two factors will be considered separately in the discussion. In this section, the information will be presented and the attempt made to define the distributions in broad terms.

It should be remembered that, compared with the 1938–39 material, the plankton has been analysed in much less detail. Minor fluctuations in estimated numbers, of the order which appeared to be significant in the earlier material, must now be disregarded as they are less than the errors involved in the present method of analysis. Of the four generations in a year recognized in 1938–39, the first of the two spring generations and the winter generation might not have been recognized had the present method of analysis then been used.

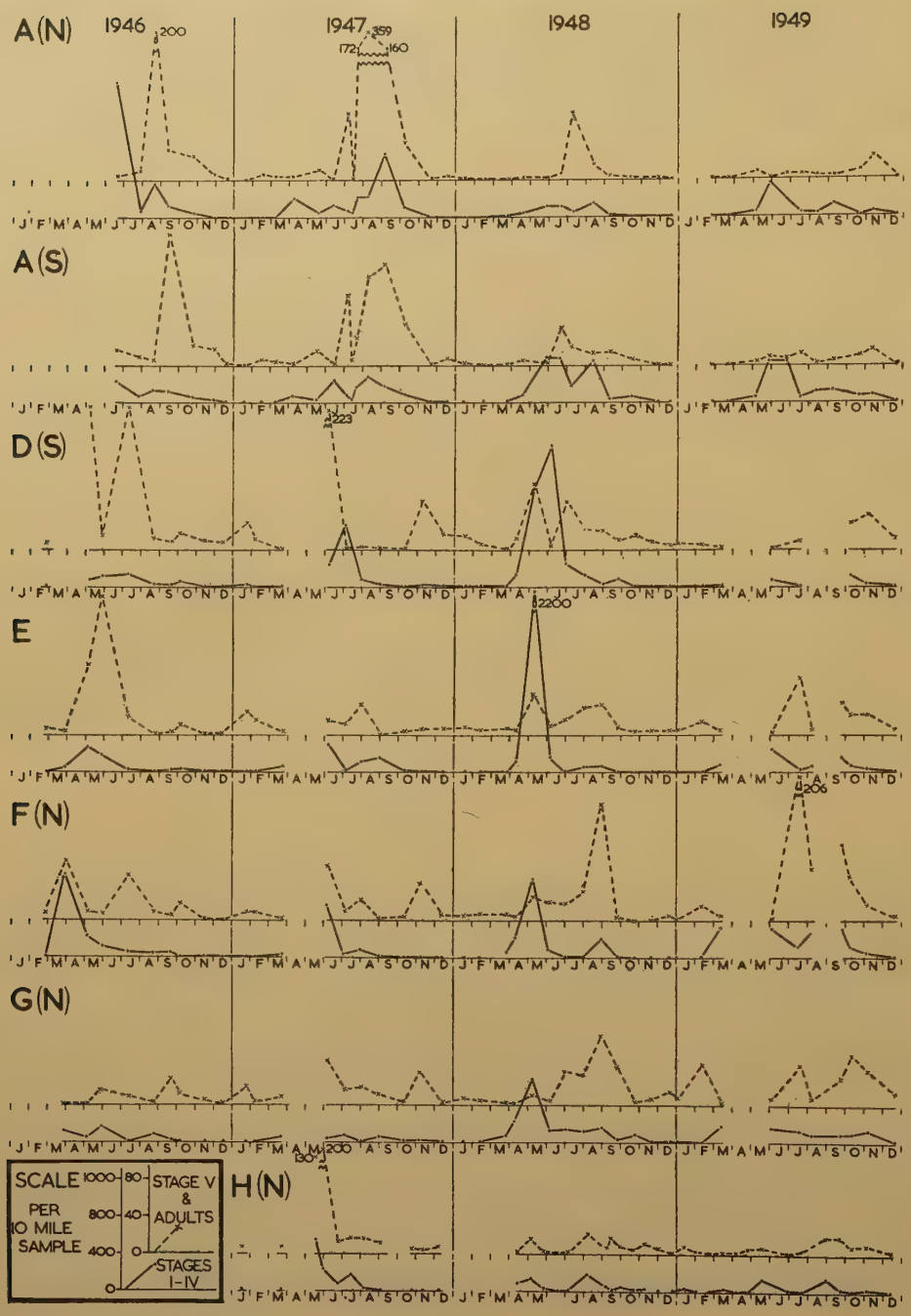
North Sea.

When dealing with the data for 1938–39 from the viewpoint of the life history, it became necessary to sub-divide the arbitrary areas used in the North Sea in order to avoid mixing populations which were clearly different. The sub-areas, which are retained in this report, are shown in Text-fig. 9.

For these sub-areas, the average numbers of young Calanus (Stages I–IV) and of late Calanus (Stage V and adults) per 10-mile sample per record are shown in Text-fig. 10. Gaps have been left in the graphs when the time interval between records was more than one and a half months. Only averages based on three or more samples are given.

The distributions of concentrations of *finmarchicus* and *helgolandicus*, Stages V and adults combined, are shown in Plates I–IV. It should be remembered that population densities of less than 9 per cu. m. (26 per 10-mile sample) are not shown in the charts. One must, therefore, not be deceived into thinking that the absence of a *helgolandicus* concentration in any month, for example, means that the form was absent or even that it was everywhere very scarce.

Text-fig. 11 consists of an abstraction from Text-fig. 10. The months in which maximum numbers of young Calanus were obtained are indicated by rectangles, a black rectangle for the greatest average number in an area during the year and

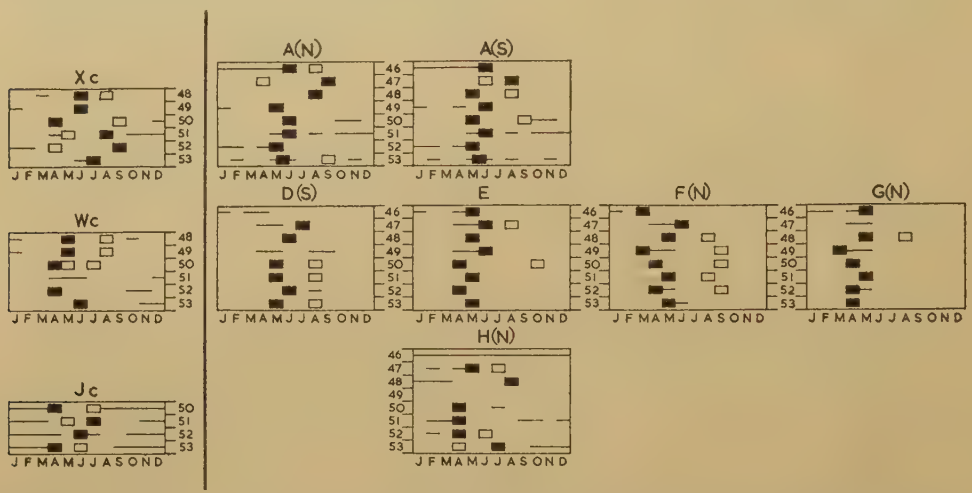


TEXT-FIG. 10.—Graphs giving the average number per 10-mile sample per record of Calanus copepodids I–IV (solid line) and Stage V and adults combined (broken line) in the subdivisions of the North Sea illustrated in Text-fig. 9. The scale is shown in the bottom left corner. The graphs and base lines are interrupted when records were more than one and a half months apart.

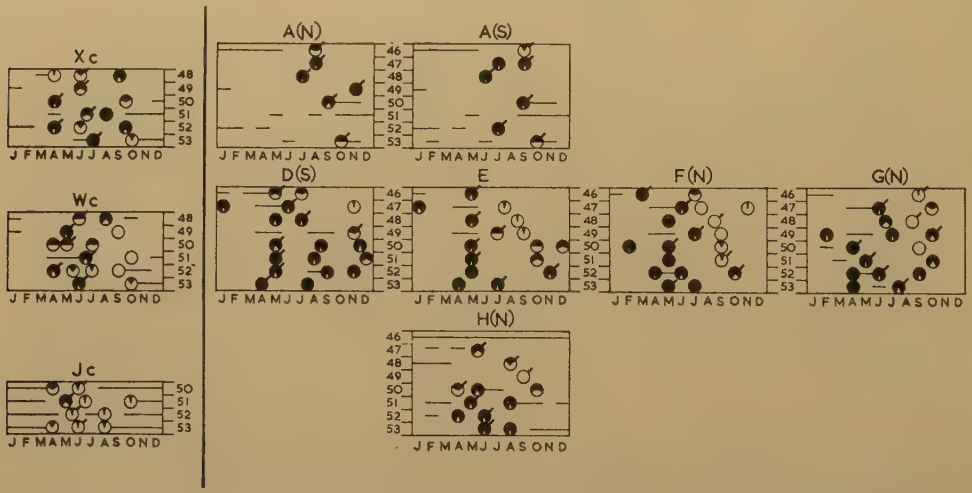
A(N)
1950
1951
1952
1953
A(S)
D(S)
206
231
E
270
3700
2340
F(N)
227
360
2910
156
3520
G(N)
H(N)

TEXT-FIG. 10.

open rectangles for secondary maxima. Maxima with an average of less than 150 individuals per 10-mile sample have been ignored. Horizontal lines indicate months in which no records were obtained. When a horizontal line is joined to a rectangle it means that the maximum might have been correspondingly displaced along the time scale ; thus a line in May joined to a rectangle in June shows that a peak in numbers occurred in May or June.



TEXT-FIG. 11.—Diagram giving the months in which peak numbers of *young* Calanus, Stages I–IV, occurred in the various areas during the years 1946–1953. The higher peaks are indicated by black rectangles and secondary peaks by open rectangles. Horizontal lines mark months in which no information was available.



TEXT-FIG. 12.—Diagram showing by circles the months in which peak numbers of *late* Calanus (Stage V and adult) occurred in the various areas during the years 1946–1953. In each circle the relative proportions of *finmarchicus* and *helgolandicus* are indicated respectively by the black and white portions. The higher peaks are marked by a dash at the 2 o'clock position and the horizontal lines mark months in which no information was available.

Text-fig. 12 is also based on Text-fig. 10; here the circles indicate months of maxima of late stages and primary maxima are shown by the tick at 2 o'clock position. Maxima involving less than 20 per sample have been ignored. The circles are divided into black and white portions according to the estimated proportion of *finmarchicus* and *helgolandicus* respectively in the peak population.

Young stages.

In nearly all cases, the primary maxima of young stages occurred in spring and usually the numbers then found far exceeded those at other times of the year. The important exceptions to the great predominance of the spring population occurred in the north-west, areas A(N) and A(S), and off the Humber, area H(N). Although the primary maxima usually occurred in spring in these areas (Text-fig. 11), the numbers obtained were low and not so greatly in excess of numbers obtained at other times of the year (Text-fig. 10). This resemblance between the Aberdeen–Lerwick route and the region off the Humber in the spring is borne out, not only by the relative poverty of the Calanus of spring, but also by other properties of the plankton such as the abundance of the neritic copepods *Temora longicornis* and *Centropages hamatus* prior to July.

There is a difference in timing of the spring generation. The maxima in the north-west and off the Forth [A(N), A(S) and D(S)] tended to occur in May to June, in the central and eastern regions [E, F(N) and G(N)] in April to May and off the Humber [H(N)] in April.

Of the secondary maxima, particular attention need be drawn only to those of August to September over the Great Fisher Bank [F(N)]. These maxima, as will be seen, are probably made up mainly of young stages of *helgolandicus*.

Late stages.

Plates I–IV emphasize two main features. The first is that concentrations of late stages of *finmarchicus* occurred mainly within the period April to July, and those of *helgolandicus* in August and September. The second is that concentrations of *helgolandicus* were much more widespread in the four years 1946 to 1949 than in the succeeding four years.

The distributions of the two forms differ so much that they must be considered separately.

Form *finmarchicus*.—When the distributions from year to year are compared, a most important difference emerges, which is illustrated by the distributions of 1950 and 1953. In 1950 the main concentrations of *finmarchicus* in the central part of the North Sea, along the whole length of the Leith–Skagerrak route, were found in May. In 1953 the main concentrations fell in July; these were more extensive and with higher numbers than in April and May. When each year is considered in the light of this difference it is seen that 1946, 1948, 1951 and 1952 resembled 1950. Since there were no Leith–Skagerrak records for April and May

in 1947 and 1949 we cannot make a proper comparison in these two years, but on the July records alone it seems likely that they resembled 1950 and 1953 respectively.

Apart from this difference between two groups of years, it is possible to recognize a normal distribution more or less common to all years. There were few concentrations of late stages in the north-west during spring; it was in summer or autumn that the main populations were found there. In spring (April to May) concentrations were found along the eastern half of the Dogger Bank; that is, mid-way along the Hull–Copenhagen route. After the main concentrations of the year in the central North Sea only a few narrow patches were found, chiefly near the Firth of Forth to begin with and then further to the east until they were found near the Great Fisher Bank around February.

This normal distribution was not, of course, followed exactly in each year. Amongst the divergences from normal distribution we may note particularly the extensive concentrations of *finmarchicus* along the Leith–Skagerrak records of September to November 1952 (Plate IV). We may note, too, the absence of concentrations in the north-west in the autumn of 1948. The marked tendency for the spring concentration on the Hull–Copenhagen route to occur only over the eastern Dogger was not observed in May 1947 when rich concentrations extended eastwards from the Humber.

The apparent scarcity of *finmarchicus* in the north-west in spring, a feature which agrees well with the relative poverty of the spring generation of young stages may be in part due to the south–north direction of the line. There were occasions when *finmarchicus* concentrations were found when a west–east record was obtained in the area; March and May 1952, April 1953 (Plate III). Such west–east records were infrequent.

In area D(S), off the Firth of Forth, there were usually three peaks in late Calanus through the year, a major one around May, a second one around July to August and a third in November to December (Text-figs. 10 and 11). These three peaks were very consistent, for only in 1947 out of seven years (1949 was inadequately sampled) was the second peak not observed, and only in 1948 and 1953 out of eight years was the third not observed; the third peak of 1946 was delayed until January 1947 (*cf.* January 1947 with December 1950). The sequence of these peaks is best exemplified in 1950.

Whereas in D(S) there were three peaks in each of the four years, 1946, 1950–52, in each of these same four years there were only two peaks in the adjacent area E (including January 1947) which corresponded in time with the first and third of D(S).

Plates A–D show that the second peak in D(S) often resulted from a concentration of *finmarchicus* which extended only a short distance offshore, not so far as area E. Good examples are to be seen in July, 1946, July to August, 1948, August to September 1950, and August 1951. The third peaks were largely due also to *finmarchicus* concentrations which were, as in the examples of the summer concentration, rather narrow. These winter concentrations, however, tended to be farther to the east and lay partly in D(S) and partly in E. Good examples are January 1947, November to December 1949, November to December 1950, November 1952.

Similar narrow concentrations occurred late, in January and February (1949–51 and 1953) which were still farther to the east. This easterly shift of *finmarchicus* brought the concentrations within range of area F(N). One may see in the graphs of Text-fig. 10 that slight peaks

of late Calanus were obtained in area F(N) in January to February in 1947, 1949–52 though the numbers did not reach the level which warrant abstraction into Text-fig. 11.

The main *finmarchicus* concentrations on the Hull–Copenhagen line occurred, in general, in April and May and they were found along the eastern half of the Dogger Bank. There was no recurrence, even at the lowest level, of the east Dogger concentration after its disappearance around June ; such concentrations as occurred were found usually close to the Humber (July 1947, September 1948, September to October 1950, August 1951, August 1953).

Form *helgolandicus*.—In general, there were only a few rather narrow and isolated concentrations of *helgolandicus* in the first half of each year, and in August and September they became much more extensive. It appears possible to resolve the concentrations, as sampled, into four centres. On the Leith–Skagerrak route there was a central one over the Great Fisher Bank, and another in, or near, the Skagerrak. On the Hull–Copenhagen line there was a central one, over the east Dogger, and another off the Danish coast. It is very likely that the Great Fisher Bank and eastern Dogger populations were linked, as were also those of the Skagerrak and the Danish coast. Through October to December the concentrations became fewer and less extensive.

In 1946 *helgolandicus* was exceptionally abundant ; it was, in fact, much more abundant than *finmarchicus* in the north-west and the concentrations of May and July were, elsewhere, very rich and extensive. It has been noted that *finmarchicus* was unusually abundant off the Humber in May 1947 ; concentrations of *helgolandicus* were also displaced from their usual position, the eastern Dogger Bank.

The concentration of *helgolandicus* over the Great Fisher Bank was sometimes narrow, as in August 1947, August to September 1950 and September 1951. At other times the concentration extended towards the west, into area E, and eastwards towards the Skagerrak population as in August 1948, September 1949 and September 1951.

That there is a centre of development inside the Skagerrak is suggested by the distributions of August 1947, September 1948, September 1950 and August 1952.

Such a distribution as that of September 1948 suggests that the Skagerrak and Danish coast populations are continuous.

The relation between young and late stages.

(*a*) The whole of the information for areas D(S) to G(N) came from the Leith–Skagerrak records and, in consequence, these areas may be closely compared regarding timing (Text-fig. 10). It then appears that the western area D(S) can be broadly distinguished from the eastern areas, E and F(N), as regards conditions in the spring.

In D(S) the primary maxima of young stages tended to be small and to follow the maxima of late stages. In E and F(N) the primary maxima of young stages were greater and tended to precede those of the late stages.

In view of the tendency for the young stages to occur mostly in the eastern half or three quarters of the Leith–Skagerrak route, it is of interest that the main concentrations of late stages of *finmarchicus* tended to occur in the western half.

The comparison between the adjacent areas D(S) and E illustrates the difference in succession of young and late stages (Text-fig. 10). The primary maximum of young stages occurred earlier in E than in D(S) in 1947, 1948, 1950 and 1952. The numbers comprising the primary maxima were lower in D(S) than in E in 1948, 1950, 1952 and 1953. Only in 1951 was there a close resemblance between the two areas ; in this year the greatest numbers were found still farther east, in F(N) and G(N). The year 1948, however, constitutes an exception for the main concentrations occurred in D(S) and E and numbers in F(N) and G(N) were much lower.

In D(S) the primary peak of young stages tended to follow that of the late stages in 1947, 1948, 1952 and 1953. In E the young stages preceded the late stages in 1946, 1949, 1950, 1952 and 1953.

The occurrence of main concentrations of late stages of *finmarchicus* in the western half is shown in 1946, 1948, 1950 and 1951. May 1953 provided a notable exception to this but in that year the main *finmarchicus* concentrations occurred in July, not in May.

(*b*) Whilst the two forms of Calanus cannot as yet be distinguished in the younger copepodid stages it is possible, in many cases, to assign the young stages to the forms by referring back from the late stages. This may be done by relating the timing of peak numbers as shown in Text-figs. 11 and 12.

There is no doubt that in the peaks of young stages during the spring *finmarchicus* predominated. Later peaks were uncommon but, as referred to above, these occurred most consistently in Area F(N) It can be seen in Text-figs. 11 and 12 that the August to September peaks here from 1948 to 1951 were undoubtedly of *helgolandicus* young stages. The September 1952 peak, however, was predominantly of *finmarchicus*. In D(S) the July to August peaks of 1950–51 and 1953 were of *finmarchicus* young stages. In the north-west, A(N) and A(S), the peaks of young stages in August to September were of *finmarchicus* in most cases but, presumably had a considerable content of *helgolandicus* in 1946 and 1953.

Coastal Atlantic.

Text-fig. 13 is arranged in the same way as Text-fig. 10 ; it gives the average number per sample on the coastal ends of the three weathership routes, X, W and J. These graphs are also abstracted on the left of Text-figs. 11 and 12 although the proportions of *finmarchicus* and *helgolandicus*, given in circles on Text-fig. 12 are very approximate.

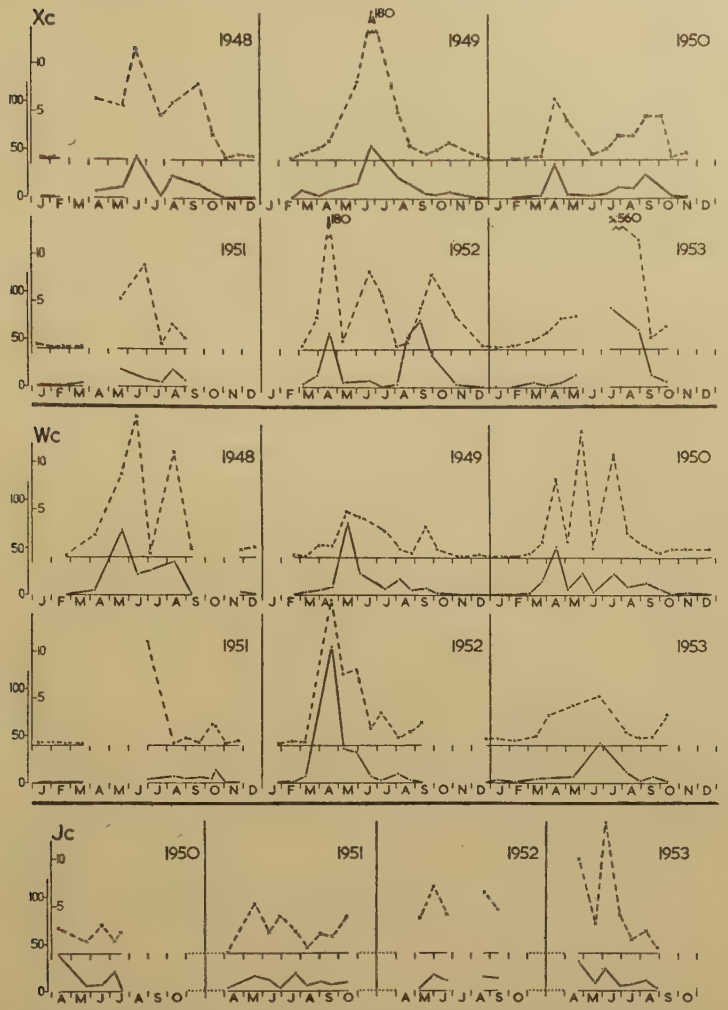
The young stages of Xc show two different sequences. In 1948, 1950–52 there were two peaks in the year, the first usually in April, but as late as June in 1948, and the second in August to September. The September peak was particularly prominent in 1952. In 1949 and 1953 there was only a single peak, in June to July.

The young stages of Wc differed mainly from those of Xc in that an August to September peak was by no means well marked. Wc differed considerably from Xc in 1949, the major peak occurring in May, but in 1953 Wc had the single June peak as in Xc.

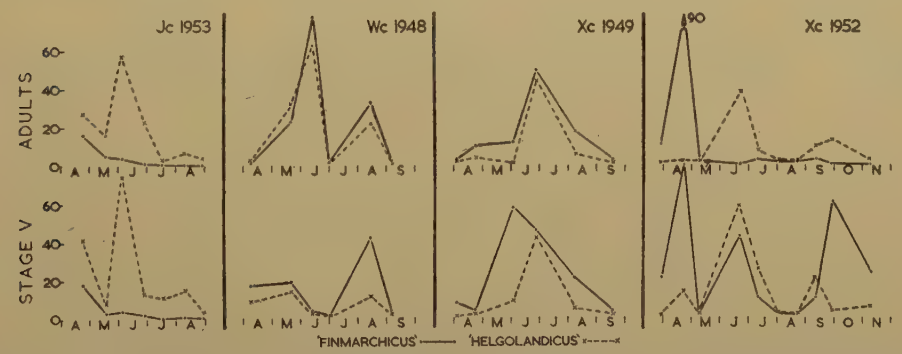
The numbers of young stages in Jc were very low. On the whole, there seem to have been two peaks in numbers between April and September, a major one in April and a minor one in June to July.

Since insufficient samples have been differentiated to allow the breaking-down of all the Atlantic concentrations into *finmarchicus* and *helgolandicus*, particular examples have been chosen and sufficient samples differentiated to allow a breaking-down not only into the forms but also into adults and Stage V. These examples are shown in Text-fig. 14.

In Jc, in 1953, the greatest number of *finmarchicus* occurred in April but even these were fewer than the *helgolandicus* ; *finmarchicus* then decreased to very low numbers which persisted until the end of August, but *helgolandicus*, on the other hand, was most abundant in June.



TEXT-FIG. 13.—Graphs giving the average number per 10-mile sample per record of Calanus, Stages I–IV (solid line) and Stage V and adults (broken line) inside the 200 m. depth contour north (Xc, Wc) and south (Jc) of Ireland. The standard routes are shown in Text-fig. 1.



TEXT-FIG. 14.—Graphs showing the average number of adults (above) and Stage V (below) of *finmarchicus* (solid line) and *helgolandicus* (broken line) per 10-mile sample in selected examples from Text-fig. 12.

One might believe that the peaks for *helgolandicus* in April and early June referred to different generations. Size measurements do not help on this point. Twenty-five Stage V specimens of each of the two peak populations were measured and these gave an average metasome size of 2·34 mm. for the April group and 2·28 mm. for the June ; such a size difference is inconsiderable. The experience from the 1938–39 results (Rees, 1949) indicates a drop in size of 0·2 mm. or more between generations at this time of year.

The curves for the two forms in Wc, 1948, are very similar in trend and so are those for Xc, 1949 except that Stage V of *finmarchicus* were most numerous before Stage V of *helgolandicus*. In Xc, 1952, there was a marked difference, *finmarchicus* being most numerous in April and *helgolandicus* in June. Neither the second nor third Stage V *finmarchicus* generation were reflected in the adults.

Oceanic Atlantic.

The monthly changes in numbers of young Calanus (black histograms) and late Calanus (hatched histograms) in the oceanic sections are shown in Text-fig. 15.

It should be explained that the weathership records from Bergen (T) invariably started at the very end of each month so that the histogram for, say, April refers to a record taken on or very near April 30th. On this route there was usually a major peak of young stages at the end of May or end of June. In 1952 the major peak was obtained at the end of April earlier than in the other years. In four years out of five there are indications of a secondary peak in August to September. The numbers of late stages were usually high from April to June. In three years out of four (1949 was incompletely sampled) there was an earlier peak at the end of April and a later one at the end of June. This feature suggests that the two peak populations are related as parents and offspring. There are indications of yet another peak in August to September or even in October (1952).

There were many gaps in the V records. The incomplete data suggests a major peak of young stages in May to June and a minor peak in July to August. In the two years with most data, 1951 and 1952, a secondary peak of late stages occurred in July and September.

Regarding the remaining three oceanic sections, X(o), W(o) and J(o), we need only refer to the overwhelming predominance of the populations in May and June.

Yearly Variations in Numbers.

As indicated above (p. 212), the individual estimates of average number of specimens per sample per year are not very satisfactory in the case of Calanus. A more satisfactory method of judging relative abundance from year to year is to consider the levels shown in Text-figs. 10, 13 and 15. We may, in general, regard the graphs for young Calanus as equivalent to total Calanus ; only rarely does the addition of the late stages alter the total for young stages to any appreciable extent.

The charts in Plates I–IV provide a means of comparing yearly variations in late stages of *finmarchicus* and *helgolandicus* in the North Sea.

For the present purposes we must, of course, consider the Calanus population of any one year in an area by relating it to the typical population density in that particular area, for the normal densities differ markedly from area to area. It should be remembered again that all the results refer only to those sections of the whole populations to be found at a depth of 10 m.

North Sea.

The most striking variations may be briefly stated.

There was a prolonged abundance of total Calanus in the central areas in the spring in 1952. There was a collapse of the Calanus population, both in total and in late stages, in the main part of the North Sea after August in 1953 but there are indications of a flourishing population of late stages around early October in the north-west [A(N) and A(S)].

There was a pronounced scarcity of late stages of *finmarchicus* in 1948. Numbers along the Leith–Skagerrak line were exceptionally high in May 1950 but rich populations did not persist except off the Forth [area D(S)]. The *finmarchicus* population off the Forth was, in fact, outstandingly rich in 1950.

In the north-west, *finmarchicus* was particularly abundant in the late summer of 1947. The rich concentrations of *finmarchicus* in July and August 1953, added to good concentrations in the spring, made this form especially numerous in 1953.

From 1946 to 1949 late stages of *helgolandicus* were generally abundant and especially so in 1946. From 1950 to 1953 they were much scarcer though there was some recovery in 1953.

A more detailed survey of the variations follows :

1946.—Over the region sampled, the Calanus population was generally scarce throughout the year, except for two important exceptions (Text-fig. 10). There was, unusually for the season, a very high number of Calanus in area F(N) at the end of March. In June the population at A(N) reached the greatest average density obtained in the north-west [including A(S)] during the post-war period.

Especially characteristic of the year was the very great abundance of late stages of *helgolandicus* particularly in the north-west (Plates I–IV). Late stages of *finmarchicus* were, on the other hand, no more than moderate in numbers.

1947.—The early autumn population in A(N) was particularly abundant, following upon a low spring population. In A(S) the population throughout the year was poor. There is no information on the size of the population in the central areas in spring ; from July onwards Calanus was scarce in areas D(S) to G(N). There was a relatively abundant spring population in H(N).

Late stages of *finmarchicus* were abundant in the spring and in the north-west in autumn. *Helgolandicus*, also, was generally abundant.

1948.—In A(N) the population was scarce throughout, though the adjoining area A(S) had abundant spring and autumn populations. The spring population in D(S) was abundant, but Calanus was scarce thereafter. In E, which was quite similar to D(S), the spring abundance was of shorter duration. Both the spring and autumn populations were only moderate in F(N) and G(N) and Calanus was generally scarce in H(N).

A marked feature of the year was the scarcity of late stages of *finmarchicus*. *Helgolandicus* late stages were relatively abundant.

1949.—The Calanus population was scarce in A(N) and also in A(S) after a comparatively abundant spring population. So few Leith–Skagerrak records were taken that little can be said about the central area but when numbers in F(N) are compared time for time with other years it appears that the Calanus was abundant here. In G(N) there was hardly any variation in the low numbers from July onwards. There was a scarcity in H(N).

It was a moderate year for late stages of *finmarchicus* largely due to the numbers

obtained in July. *Helgolandicus* was relatively abundant but the main population was somewhat delayed.

1950.—The population was scarce up to the end of August in A(N). In A(S) the May population was relatively abundant. The population was generally abundant in the central area, D(S)–G(N).

Late stages of *finmarchicus* were abundant and *helgolandicus* scarce.

1951.—In areas D(S) to G(N) the populations were scarce except for short but very considerable outbursts in May in F(N) and G(N). In H(N) the population was scarce to moderate.

Late stages of *finmarchicus* were moderately abundant and *helgolandicus* scarce.

1952.—The populations in A(N) and A(S) were, yet again, scarce. In the central areas the spring populations were very abundant, high numbers persisting for about three months, April to June.

Late stages of *finmarchicus* were abundant, *helgolandicus* scarce.

1953.—There was a moderate population in A(N) and scarce in A(S). The spring population in D(S) was small but there was a rich August population. The spring population was abundant in areas E, F(N) and G(N) but numbers after July were remarkably low. H(N) had a relatively abundant population.

Late stages of *finmarchicus* were very abundant, especially in July and August. It was a moderate year for *helgolandicus*. As in the case of total Calanus, the late stages of Calanus were very scarce after August.

Coastal Atlantic.

The graphs of Text-fig. 13 may be used to judge overall yearly populations in the coastal Atlantic areas. Such estimates as may be derived are much more tentative than in many cases in the North Sea.

The data are insufficient to allow a distinction between late stages of *finmarchicus* and *helgolandicus*.

Oceanic Atlantic.

The yearly fluctuations are shown in the histograms of Text-fig. 15, and it would seem that Calanus was most abundant in area T in 1952. In Xo, also, 1952 had the most Calanus but not outstandingly so. The population was relatively scarce in 1950. In Wo 1952 and 1953 had the greatest population, 1949 and 1950 being years of scarcity. In Jo most Calanus were obtained in 1953, and least in 1950.

Discussion.

In this report on Calanus we are concerned with the *general* distribution of the two forms *finmarchicus* and *helgolandicus*. There remain several features of distribution which require a more intimate study and it is hoped that an opportunity of dealing with some of these will arise at a later date.

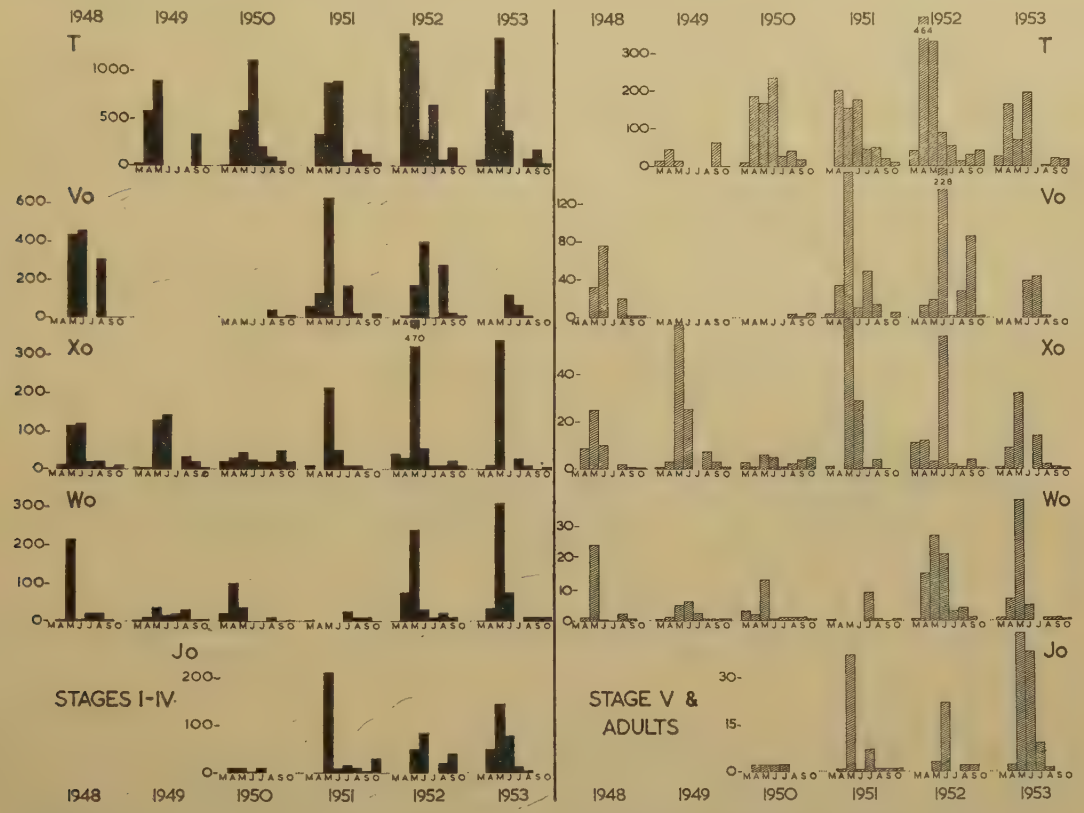
Life-history.

The more detailed work in the North Sea during 1938–39 indicated that four generations of Calanus in the year could be recognized. The generalized scheme of succession is shown in Rees (1949, Text-fig. 12). Simplifying this further, so as to

conform with the present grouping into young stages (Stages I–IV) and late stages (Stage V and adults), we obtain the following monthly sequence of generations :

	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.
Late stages . . .	—	4/0	—	1	—	—	2	—	—	3	—	—
Young stages . . .	—	—	1	—	2	—	—	3	—	—	4	—

The north-west did not conform to the main part of the North Sea in this sequence and timing of generations.



Text-fig. 15.—Giving the average number per 10-mile sample per month of Calanus, Stages I–IV (black histograms) and Stage V and adults (hatched histograms), along the Norwegian Sea route (T) and outside the 200 m. depth contour along the Atlantic routes. The standard routes are shown in Text-fig. 1.

When the separate forms were considered it was found that the third and fourth generations of *finmarchicus* were recognizable only in the northern North Sea and in the Skagerrak. There was, in fact, no evidence of a third generation of *finmarchicus* in the western and central areas (Rees, 1949, p. 249). The second and third generations of *helgolandicus* were the main ones.

The numbers in one or two of the generations were too low to be revealed by the method of plankton analysis now employed, so that no complete comparison

between the post-war and pre-war results can be made. Furthermore, too few samples were taken in the northern North Sea to provide adequate information on the life history there.

Finmarchicus.—In the account given above (p. 229), distinction was drawn between two patterns of distribution as illustrated by the years 1953 and 1950. In 1953 the main concentrations of late stages in the central North Sea occurred in July. Extensive concentrations occurred also in spring, those of April being somewhat more pronounced than those of May. In 1950 the main concentrations occurred in May, there being few in July.

It is clear that 1953 resembled 1938–39 in the distributions and that 1950 did not.

With some reservations, most of which are connected with missing records, we can say that the years 1938, 1939, 1949 and 1953 conformed to one pattern, and the years 1946, 1947, 1948, 1950, 1951, and 1952 conformed to the other. The most likely explanation for the difference between the two is that there were two spring generations in the first group, as indeed could be shown in 1938–39, and only one in the second group. Only a single spring generation was recognized off the Humber [area H(N)] in 1938–39 (Rees, 1949, p. 248).

The difference is of great importance since in the one case rich concentrations of late stages are obtained in April to May and July to August, in the other case only in April to May.

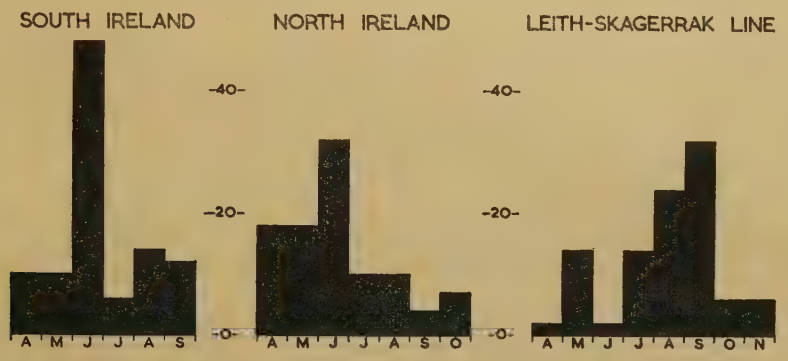
When the distributions are looked at more closely it is seen that the area off the Forth [D(S)] may conform to the 1938–39 distributions when the central area E and F(N) do not. It was pointed out above (p. 231) that there was a tendency for the succession to be :

In E and F(N) :	Young Stages —→	Late Stages
In D(S) :		Late Stages —→ Young Stages

The concentrations of *finmarchicus* off the Forth in July and August may have originated locally from these young stages. It would appear that we must accept this as the most likely explanation for the concentrations in July and August 1948 (Plates I and II, and Text-fig. 10). However, as will be referred to below, the indicator forms of mixed oceanic-North Sea water usually reach the Forth area in August and the *finmarchicus* concentrations may be involved with this transport. This would appear to explain most satisfactorily the concentration of August 1951 (Plate IV, and Text-fig. 10). In 1950 the August concentration was so closely related to indicator forms (see also below) and so well developed that its having arisen in that locality seems unlikely. A point of importance is that the climax of late stages of the second spring generation is to be expected in early July.

As in D(S), concentrations of *finmarchicus* were sometimes found near the mouth of the Skagerrak in July in years when concentrations were absent in the centre of the Leith–Skagerrak line.

The concentrations of *finmarchicus* in the central North Sea from September onwards in 1952 constitute an interesting exception to the normal patterns of distribution. These were preceded by a peak of young stages [see F(N) in Text-fig. 10] and fit in exactly with the third generation found in 1938–39, though only in the northern North Sea. These young stages could not have come from the late stages of May found in great numbers in the same area. The complete cycle of a generation of Calanus in the North Sea was estimated at 70–80 days (Rees, 1949, p. 253), an estimate that agrees well with that of other workers. The major peak of young stages was in mid-April [E and F(N) in Text-fig. 10]. About 90 days later young stages were exceedingly scarce, 120 days later they had increased in number and reached the peak about 150 days later. There was, in fact, time for an intervening generation, although there was no indication of it along the centre of the Leith–Skagerrak line.



Text-fig. 16.—Histograms giving the percentage in each month of all samples estimated to contain more than 50 Stage V and adults of *helgolandicus* south and north of Ireland and along the centre of the North Sea.

Helgolandicus.—The results for *helgolandicus* in the North Sea resemble the findings for 1938–39 when the main generation was the summer one, the greatest number of late stages being obtained in October (Rees, 1949, p. 232).

The reproductive cycle of *helgolandicus* in the North Sea differs markedly from that in the coastal Atlantic areas where the spring generation is the major one. This difference is brought out clearly in Text-fig. 16 which shows the percentage in each month of all samples estimated to contain more than 50 *helgolandicus*. South and north of Ireland the highest percentage occurred in June, in the North Sea in September. The secondary peak in May in the North Sea doubtless originated from a spring reproduction which was clearly less intense than the summer one. That a spring generation can occur in the North Sea is apparent from the 1939 results in which it is possible to follow Stage IV *helgolandicus* through to Stage V and adults in the spring (Rees, 1949, Text-fig. 13).

Water movements.

Form *finmarchicus*.—There is no doubt that, as Farran (1911) maintained, the distribution of Calanus in the North Sea is under the influence of water entering the area from the north. This is shown in two ways, firstly by transporting Calanus into the North Sea and within it and secondly by providing a favourable environment for reproduction inside the North Sea. Fraser (1937) has pointed out that one of the characteristics of mixed oceanic and coastal water is its rich Calanus content.

The two effects of this influence obscure each other and often an incoming population is indistinguishable from one developing locally. When the expected sequence of development of a population in an area is disturbed, however, the effect of physical transport may be recognizable, especially when the disturbance can be related to other " indicator " species. The influx of young stages into the north-west and Forth area in July 1938 is a good example of this (Rees, 1949, p. 255).

While there has not been, in post-war years, an invasion of young stages into the north-west North Sea on a scale comparable to that just referred to, an influx of late stages of *finmarchicus*, similar to that believed to have occurred in August 1938 (Rees, 1949, p. 255), appears to have been fairly regular, though it might be later than than August when the main population arrived. The view that these late stages of the autumn were the results of normal development of a local population is unacceptable, for their numbers were much greater than in spring, which is quite contrary to the usual course. Everywhere else, from south of Ireland to the Norwegian Sea and inside the North Sea, the spring generation was much greater.

It was noted above that the *finmarchicus* population of the spring and that of September to October 1952 in the central North Sea were separated by too great an interval of time to be related as parents and offspring. There was, in fact, time for two complete generations and there was no trace of even one. It is of interest to consider this period of 1952 in comparison with other years.

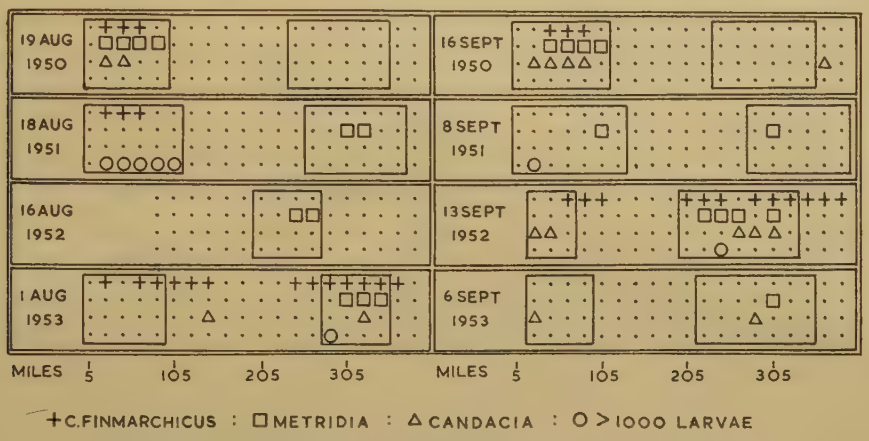
Text-fig. 17 illustrates the distribution of some forms along the Leith–Skagerrak records of August and September in each year from 1950 to 1953. In order to keep the picture simple, only a few forms are included. The distribution of *finmarchicus* concentrations are repeated from Plate IV. Samples containing *Metridia lucens* and *Candacia armata*, which are indicator species of mixed oceanic and North Sea water, are shown. Since the occurrence of heavy concentrations of lamellibranch larvae has already been discussed (Rees, 1954), the samples containing over 1000 larvae are also shown. *Metridia lucens*, during this period, is obtained almost entirely in samples taken at night ; they are enclosed in rectangles in the text-figure.

In August and September 1950 the association of *finmarchicus* with *Metridia* and *Candacia* is very well shown.

In August 1951 the *finmarchicus* concentration coincided with a heavy

concentration of lamellibranch larvae. Larvae of *Mytilus edulis* were predominant and it has been concluded that these larvae must have originated somewhere to the north of the area sampled (Rees, 1954, p. 42). As just mentioned above, this concentration of *finmarchicus* does not fit in with the sequence of development of a local population. In September 1951 there were no *finmarchicus* concentrations and the indicator forms were very scarce.

The distributions of 1952 were unusual in that there was an increase of indicator forms in the east in the September record. It is usual at this time of year for these forms to increase off the Forth, whilst any indicator forms found in the east appear to be remnants of an earlier invasion. The occurrence of a concentration of lamellibranch larvae about 260 miles from the Forth is of special interest and the repeated



TEXT-FIG. 17.—Symbols show the samples containing (*a*) over 25 Stage V and adults of *finmarchicus*, (*b*) *Metridia lucens*, (*c*) *Candacia armata*, (*d*) *over* 1000 lamellibranch larvae in the Leith–Skagerrak records of August and September of 1950 to 1953. Samples taken at night are enclosed in rectangles.

occurrence of a concentration of larvae at this place has received particular attention. That the concentration should occur in September is, however, very unusual; in all other examples it has been obtained in early July or earlier. These concentrations are believed to be associated with mixed oceanic and North Sea water (Rees, 1954, p. 44). From both aspects, the life history and distribution of indicator forms, the *finmarchicus* concentrations of this month appear to be due to invasion.

The August record of 1953 was taken earlier, July 31st to August 2nd, than the corresponding records of the other years. The *finmarchicus* concentrations are best considered as the declining population of the second spring generation. By September 6th indicator forms were scarce and they were just as scarce on the record of September 20th.

There is little doubt that the concentrations of *finmarchicus* off the Forth in November and December are the result of transport. As previously mentioned there is a tendency for concentrations to be found farther and farther to the east

through the winter months. This corresponds to a similar tendency in *Metridia lucens* which is now being investigated.

The importance of this easterly shift is shown by subsequent events. It was mentioned breifly above that there was a marked tendency for the greatest numbers of young stages of spring to occur in the eastern half or three quarters of the Leith–Skagerrak route. This fits in well with the placing of the invading late stages of *finmarchicus* at the end of winter and is a pointer to the importance of the invading population in the North Sea. What is by no means clear is why the late stages, those of May, arising from these young stages failed to reproduce extensively in most years. The late stages of May off the Forth did so but there was no earlier abundance of young stages here. It would seem that only one heavy reproduction of a population can occur during a year, possibly for a reason connected with the phytoplankton food supply.

Attention may be drawn here to the usual occurrence of *finmarchicus* concentrations along the eastern half of the Dogger Bank in April and May. There is a scarcity of known indicator forms at this time of year so that it is, at present, difficult to provide evidence for the view that the path of mixed oceanic–North Sea water crosses the eastern Dogger Bank at this time. However, there is at least one indication that this is so. In May 1950 a concentration of *Mytilus edulis* larvae was found here and this concentration was linked with other concentrations farther to the north, which appeared to be associated with mixed water (Rees 1954). A concentration of *finmarchicus* coincided with this larval concentration (Plate III).

Form *helgolandicus*.—The North Sea distribution of this form in 1938–39 was thought to resemble that of the central North Sea species *Labidocera wollastoni* and *Isias claviceps* (Rees, 1949, p. 230), the implication being that *helgolandicus* is a member of the *Sagitta setosa* community. The wider knowledge now available does not support this, for *helgolandicus* is much more common in the water over the Atlantic Continental Shelf, than in the North Sea, and it is somewhat more common on the Leith–Skagerrak route than on the Hull–Copenhagen one (Table II, p. 218). This sort of distribution is unlike that to be expected of a typical member of the " setosa " community.

It is suggested that the distribution of *helgolandicus* in the North Sea is, as in the case of *finmarchicus*, also influenced by water coming in from the north. There is, however, an important difference between the two forms. Whilst *finmarchicus* is sometimes carried in with the northern water it seems unlikely that any appreciable amount of *helgolandicus* is thus brought. This appears so because of the respective population densities of the two forms in the northern approaches to the North Sea, that of *finmarchicus* being high and that of *helgolandicus* being low. The distributions in 1946 may suggest an invasion of *helgolandicus* (Plates I and II) but these distributions were undoubtedly unusual and, if *helgolandicus* was brought in then, the most likely explanation is that the invading water came from an unusual source.

The suggestion is rather that the influence of the northern water is reflected by it providing a suitable environment for the development of a *helgolandicus* population. Since it takes time for a population to develop there is a delay between the formation of the favourable environment and the climax of the development. An analysis of the distribution of lamellibranch larvae, in association with some indicator forms, led to the conclusion that mixed oceanic–North Sea water is often centred near the Great Fisher Bank in the beginning of July (Rees, 1954). This mixed water is usually low in content of *finmarchicus* but gives the favourable conditions for the development of *helgolandicus* concentrations here around September. On the Hull–Copenhagen line concentrations of the two forms frequently coincided, even in April. Later on the main concentrations were found over the eastern half of the Dogger Bank, in the same place as the *finmarchicus* concentrations of spring (Plates I–IV).

Certainly *helgolandicus* must be carried about in the North Sea by the current system ; the unusual concentration off the Firth of Forth in November 1947 is very likely an example of this (Plate II). The form is probably carried out of the North Sea in the Baltic current along the coast of Norway since there appears to be a centre for *helgolandicus* inside the Skagerrak.

The distribution in the Atlantic.

The discussion has taken little account of the distributions outside the North Sea. To some extent, this will be rectified when some special aspects are considered in a later report. It is proposed now only to suggest, in general terms, some principles underlying the Atlantic distribution.

A consideration of the distribution of *finmarchicus* in the open Atlantic must take into account the work of Sømme (1934) on its behaviour off Lofoten, and the conclusions he drew therefrom. Sømme found that *finmarchicus* spends the winter in deep water, rises to the surface in spring and spawns after an interval of two months. He then concluded that two factors determine its spawning area, the winter distribution and the scattering effect of surface currents between the time of its upward migration and its spawning.

It is probable that *finmarchicus* is to be found well to the south in the Atlantic wherever deep, cold water currents bring specimens from the northern reservoir. This being so, these *finmarchicus* would migrate to the surface in late winter and, after a time, spawn if environmental factors were suitable. If the upwards migration was into water flowing swiftly to the north the copepodid offspring would not appear until some hundreds of miles north of the place of surfacing of the parents because of the time taken to pass through the nauplii stages. Even then the population would be small in comparison with that in the adjacent water, for the initial stock would be low and scattering effects would have been operating for some time. If, however, the water was relatively stable, as in an established eddy system, an abundant population might develop even as far south as Lat. 52°N. (Text-fig. 6).

According to the circulation shown by Herman and Thomsen (1946), the Atlantic recorder routes sample through both current and eddy systems. Einarsson (1954) has recently stressed the biological importance of large eddy systems in maintaining autochthonous animal stocks.

It is suggested, therefore, that, by its habit of sinking into deep water and then rising to the surface, *finmarchicus* establishes a closed circuit, in the vertical plane, in contact with a large northern reservoir. Damas (1905) used the concept of a closed circuit to explain the maintenance of Calanus stocks in the Norwegian Sea, this circuit being in the horizontal plane.

It is not known whether *helgolandicus* behaves similarly. If it did, and if there were a vertically closed circuit in contact with a large southern reservoir, such a system in our waters would be far less favourable than the one for *finmarchicus* since it would be unsuitably orientated. The south to north part of the circuit carries the *finmarchicus* into increasingly favourable conditions and towards its reservoir, whilst the *helgolandicus* would be carried into increasingly unfavourable conditions and away from its reservoir. This fact would, of course, apply even if *helgolandicus* did not sink to deep water in the autumn.

Summary.

1. A general account is given of the distribution of *Calanus finmarchicus*, and its two forms *finmarchicus* and *helgolandicus*, in the North Sea and north-eastern Atlantic, as revealed by the recorder survey from 1946 to 1953.

2. As Text-fig. 2 shows, Calanus in the North Sea was most abundant in the central area and only moderately so in the north-west. Late stages were more abundant north of Ireland than anywhere in the North Sea and about twice as abundant as in the south of Ireland (p. 216). Calanus was scarce in the southern part of the oceanic region but increased in numbers towards the north.

3. In the North Sea, the main areas for *helgolandicus* were over the Great Fisher Bank and along the eastern Dogger Bank (Text-fig. 4). Another centre for *helgolandicus* was the Skagerrak and off the Danish coast.

4. In the oceanic Atlantic there were few samples containing *helgolandicus* north of Rockall. Both *finmarchicus* and *helgolandicus* occurred south of Rockall in spring but, later, the former virtually disappeared (Text-fig. 6). Occasional rich samples of *finmarchicus* were found even so far south as Lat. 52°N. (Text-fig. 8).

5. In the coastal Atlantic the percentage of *helgolandicus* among late stages of Calanus decreased from south to north, being 80–90% south of Ireland, 30–50% north of Ireland and less than 20% north of Scotland (Text-fig. 7). Very approximately, the south of Ireland to north of Ireland ratio of numerical abundance of *helgolandicus* was 3 : 2 and of *finmarchicus* 1 : 6 (p. 223); *helgolandicus* was much more abundant north of Ireland than anywhere in the North Sea at 10 metres.

6. Generally, over the entire region, the greatest numbers of young stages occurred in spring, far exceeding those at other times of the year. Smaller peak numbers of young stages were sometimes found in summer, especially over the Great Fisher Bank where they were generally the precursors of concentrations of *helgolandicus* (p. 229).

7. The main concentrations of late stages in the north-west North Sea occurred in autumn. Although *finmarchicus* usually predominated, there were occasions, when *helgolandicus* was relatively numerous.

8. In the central North Sea the main concentrations of *finmarchicus* occurred in May in some years (1946–48, 1950–52). In other years (1938–39, 1953) the main concentrations occurred in early July, following fairly heavy concentrations in April and May. It is considered that there was only one spring generation in the first group of years, and two spring generations in the second group.

9. Late stages of *helgolandicus* were generally abundant in the North Sea from 1946 to 1949, and were especially so in 1946. From 1950 to 1953 they were scarce. Late stages of *finmarchicus* were relatively very scarce in the North Sea in 1948 (p. 235).

10. Whilst the seasonal succession of *finmarchicus* was fairly similar throughout the entire region of survey, *helgolandicus* had its main reproduction in spring in the Atlantic, in summer in the North Sea (p. 239).

11. It appears that mixed oceanic–North Sea water influences the distribution of *finmarchicus* in the North Sea through carrying recruits to the local stocks and through providing a satisfactory environment for local production. The influence of transport is illustrated (p. 240). It is suggested that *helgolandicus* finds such mixed water most favourable but is rarely, if ever, carried into the area by this mixed water (p. 243).

12. By applying the findings of Sømme (1932), it is suggested that the distribution of *finmarchicus* in the Atlantic may be maintained through the existence of a closed water circulation in the vertical plane (p. 243).

References.

Damas, D. 1905. Notes Biologiques sur les Copepodes de la Mer Norvegienne. Publ. Circ. Cons. Int. Explor. Mer., 22, pp. 1–23.

Einarsson, H. 1954. On the Origin and Dispersal of Icelandic Fish Population with Special Regard to the Herring. Natturufr., 24. arg., 2 hefti, pp. 60–91.

Farran, G. P. 1911. Copepoda. Bull. Trim. Cons. Int. Explor Mer, II, pp. 60–149.

Fraser, J. H. 1937. The Distribution of Chaetognatha in Scottish Waters during 1936 with Notes on the Scottish Indicator Species. Journ. du Cons. Int. Explor. Mer, XII, 3, pp. 311–320.

Hermann, F., and Thomsen, H. 1946. Drift-bottle Experiments in the Northern North Atlantic. Medd. Komm. Danm. Fisk.-og Havunder. Ser. Hydrografi, III, 4, pp. 1–87.

MARSHALL, S. M., and ORR, A. P. 1952. On the Biology of *Calanus finmarchicus*. VII. Factors Affecting Egg Production. Journ. Mar. Biol. Assoc., XXX, 3, pp. 527–548.

—— —— 1955. The Biology of a Marine Copepod. Pp. 1–188. Edinburgh.

RAE, K. M. 1952. Continuous Plankton Records: Explanation and Methods, 1946–1949. Hull Bull. Mar. Ecol., III, 21, pp. 135–155.

—— 1953. Continuous Plankton Records: List of Records, 1950–53. Bull. Mar. Ecol., IV, 25, pp. 1–20.

REES, C. B. 1949. Continuous Plankton Records: The Distribution of *Calanus finmarchicus* (Gunn.) and its Two Forms in the North Sea, 1938–39. Hull Bull. Mar. Ecol., II, 14, pp. 215–275.

—— 1954. Continuous Plankton Records: The Distribution of Lamellibranch Larvae in the North Sea, 1950–51. Bull. Mar. Ecol., IV, 27, pp. 21–67.

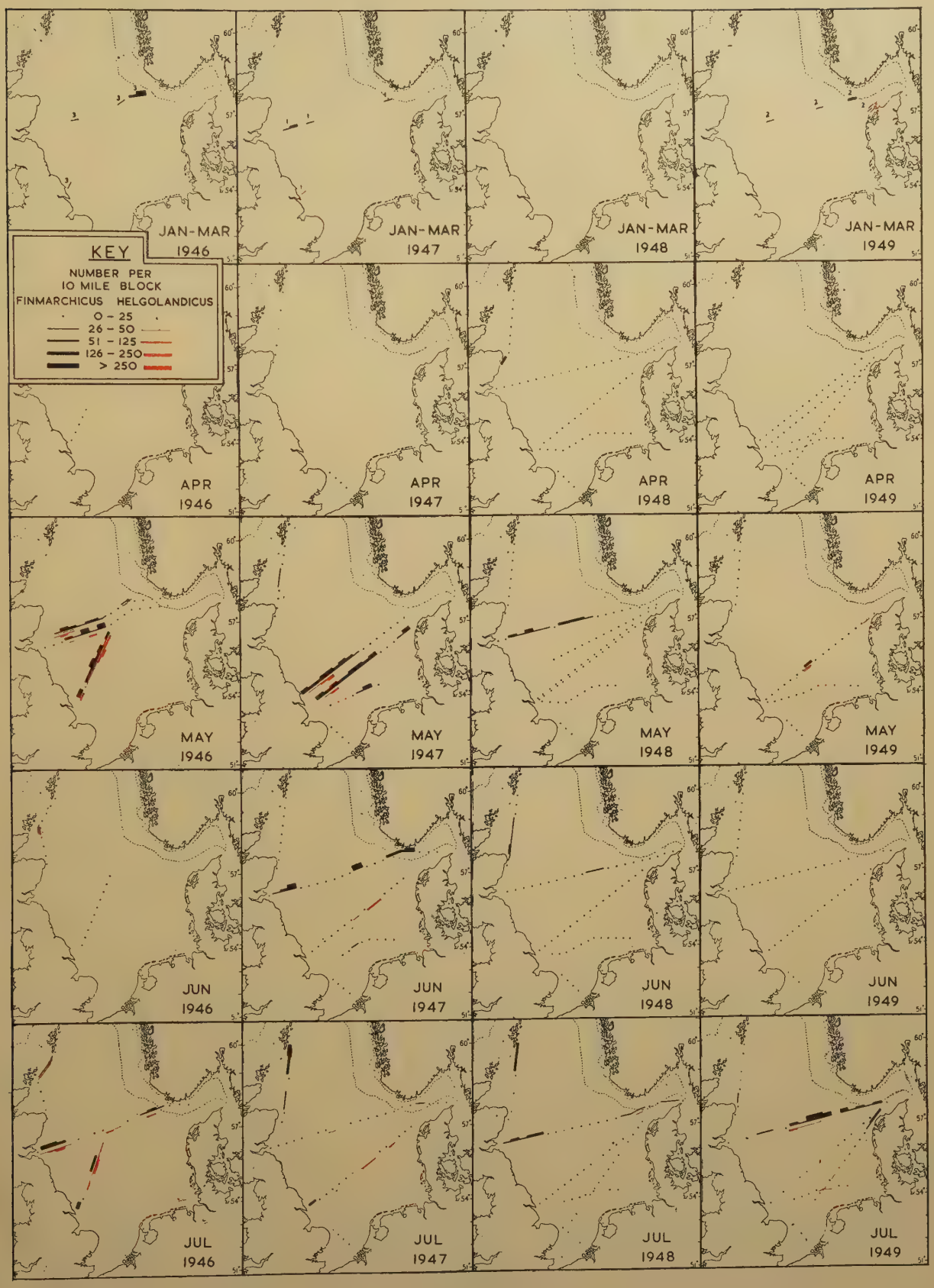
RUSSELL, F. S. 1952. A Re-examination of *Calanus* collected off Plymouth. Journ. Mar. Biol. Assoc., XXX, 2, pp. 313–314.

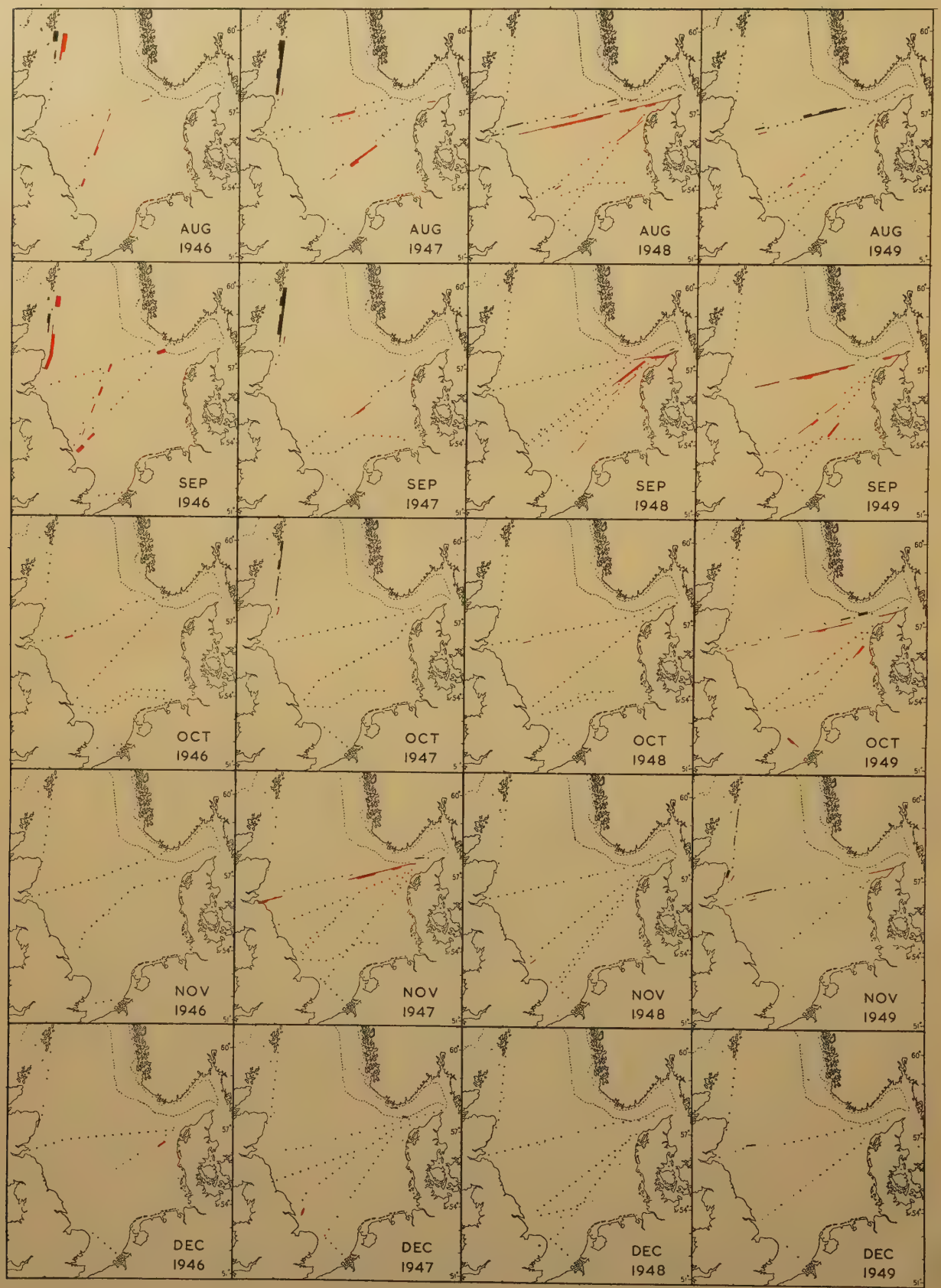
SARS, G. O. 1903. Crustacea of Norway. IV. Bergen.

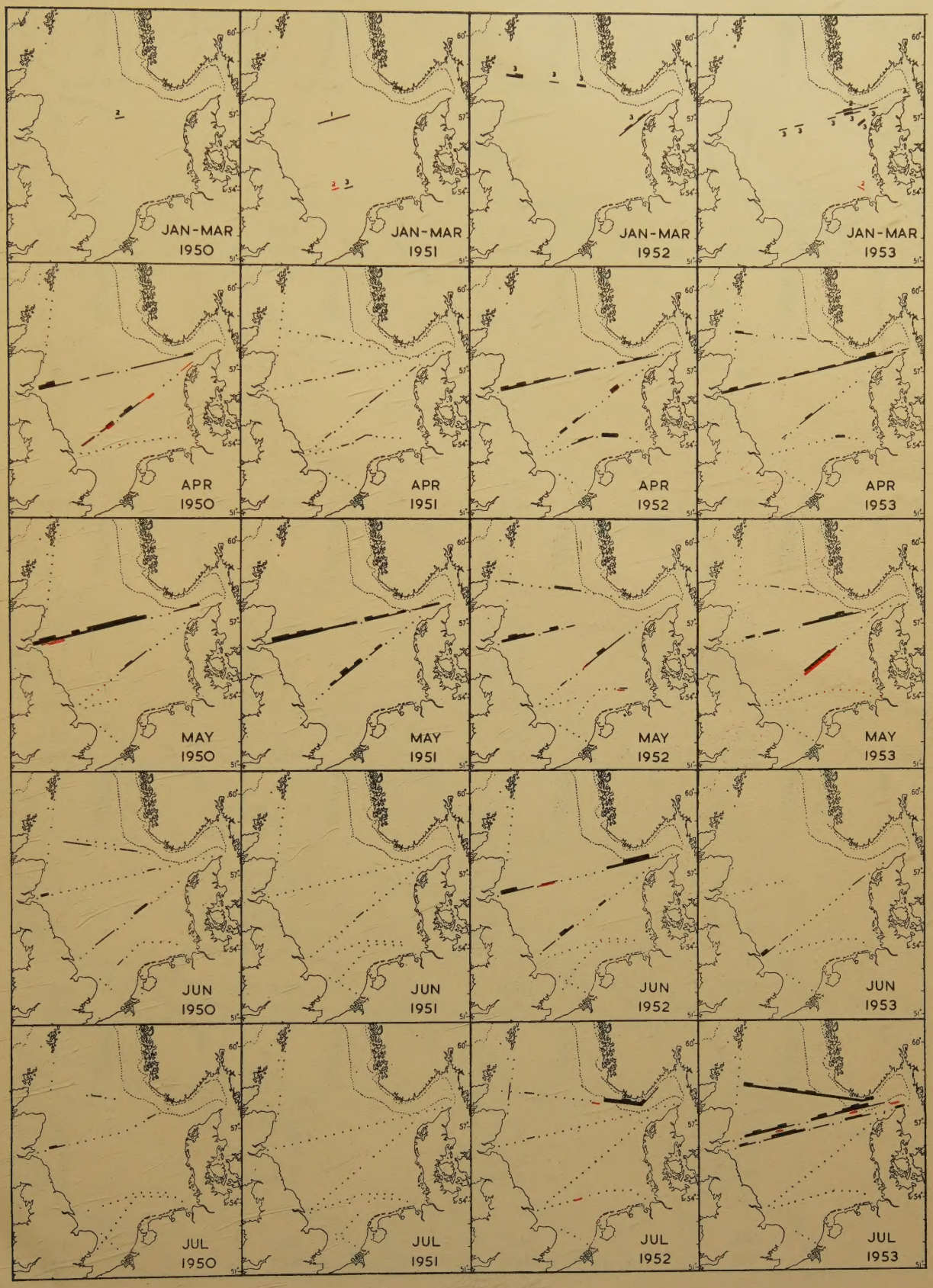
SØMME, J. D. 1934. Animal Plankton of the Norwegian Coast Waters and the Open Sea. I. Rep. Norweg. Fish. Mar. Invest., IV, 9, pp. 1–163.

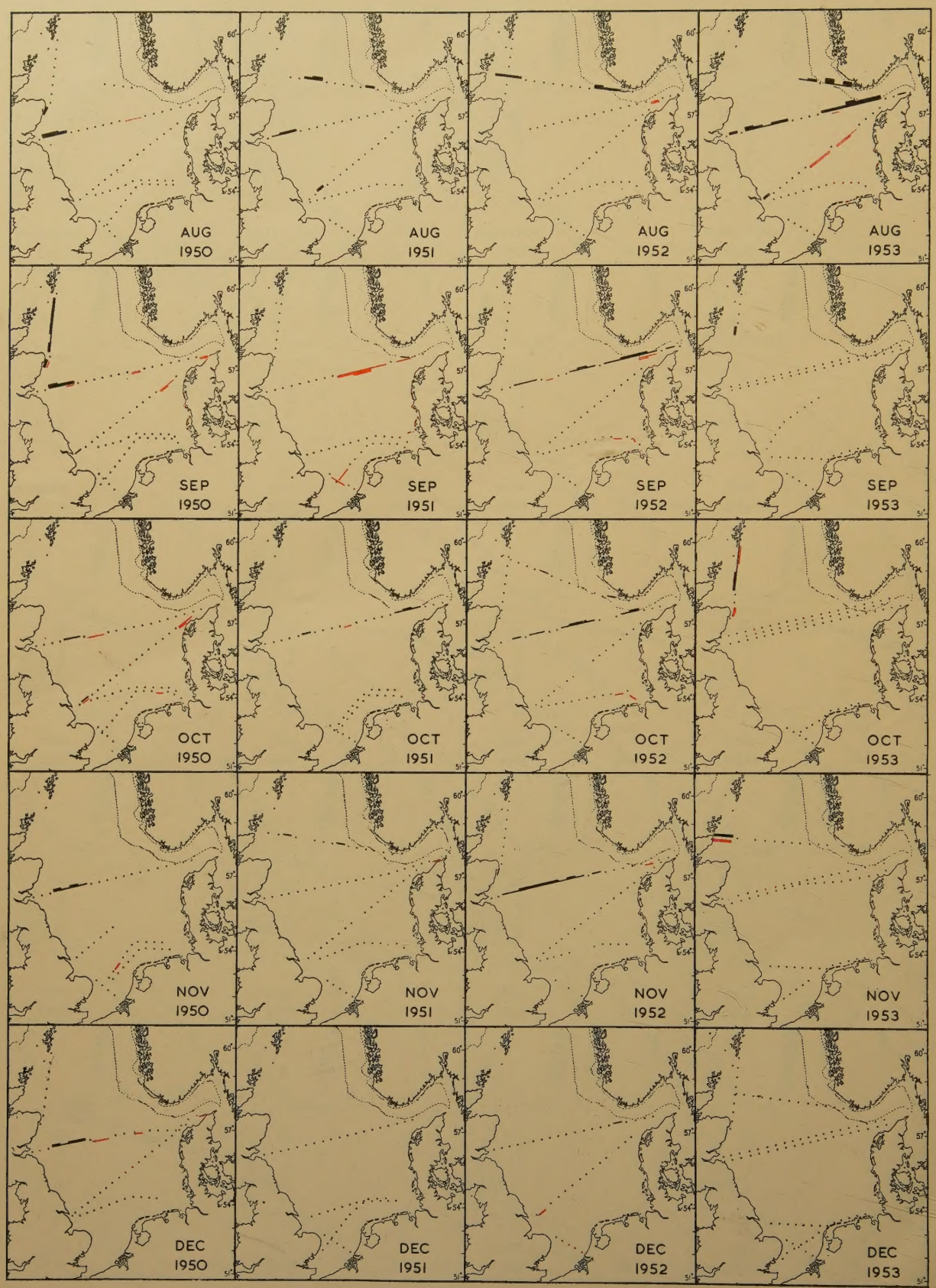
EXPLANATION OF PLATES I–IV.

A series of charts showing month by month the relative distributions of the Stage V and adults two forms, *finmarchicus* (in black) and *helgolandicus* (in red), in the North Sea during the years 1946–1953. Three months are combined in the top row of charts and in these the months of occurrence, January, February or March, are denoted by the numerals 1, 2 and 3 respectively. Elsewhere a dot indicates a sample in which not more than 25 *Calanus* were taken, while the thickness of the line shows the relative abundance of the two forms on the scale given on Plate I. A sample, or 10-mile block represents approximately 3 cu. m. of water sampled.


KEY
NUMBER PER
10 MILE BLOCK
FINMARCHICUS HELGOLANDICUS
0 - 25
26 - 50
51 - 125
126 - 250
> 250
JAN-MAR 1946
JAN-MAR 1947
JAN-MAR 1948
JAN-MAR 1949
APR 1946
APR 1947
APR 1948
APR 1949
MAY 1946
MAY 1947
MAY 1948
MAY 1949
JUN 1946
JUN 1947
JUN 1948
JUN 1949
JUL 1946
JUL 1947
JUL 1948
JUL 1949


AUG 1946
AUG 1947
AUG 1948
AUG 1949
SEP 1946
SEP 1947
SEP 1948
SEP 1949
OCT 1946
OCT 1947
OCT 1948
OCT 1949
NOV 1946
NOV 1947
NOV 1948
NOV 1949
DEC 1946
DEC 1947
DEC 1948
DEC 1949


JAN-MAR 1950
JAN-MAR 1951
JAN-MAR 1952
JAN-MAR 1953
APR 1950
APR 1951
APR 1952
APR 1953
MAY 1950
MAY 1951
MAY 1952
MAY 1953
JUN 1950
JUN 1951
JUN 1952
JUN 1953
JUL 1950
JUL 1951
JUL 1952
JUL 1953


AUG 1950
AUG 1951
AUG 1952
AUG 1953
SEP 1950
SEP 1951
SEP 1952
SEP 1953
OCT 1950
OCT 1951
OCT 1952
OCT 1953
NOV 1950
NOV 1951
NOV 1952
NOV 1953
DEC 1950
DEC 1951
DEC 1952
DEC 1953

The ' Bulletins of Marine Ecology ' are in continuation of the ' Hull Bulletins of Marine Ecology '. Copies may be purchased, or arrangements made for exchange with other publications, on application to the Officer in Charge, Oceanographic Laboratory, 78, Craighall Road, Edinburgh 5.

The following ' Bulletins ' are now published or in the press :

'HULL BULLETINS OF MARINE ECOLOGY.'

Volume I :

Nos. 1–6, with Title-page, List of Contents, Preface and Explanation 35/–

Volume II :

Nos. 7–16, with Title-page, List of Contents, Preface and Explanation 49/6

Volume III:

Nos. 17–24, with Title-page, List of Contents, Preface and Explanation 54/–

'BULLETINS OF MARINE ECOLOGY.'

Volume IV :

No. 25. Continuous Plankton Records : List of Records, 1950–53. By K. M. Rae
No. 26. The Hardy Plankton Indicator and Sampler : a Description of the various models in use. By R. S. Glover — 5/–

No. 27. Continuous Plankton Records : The Distribution of Lamellibranch Larvae in the North Sea, 1950–51. By C. B. Rees .. ..
No. 28. ——— The Distribution of Echinoderm and Other Larvae in the North Sea, 1947–51. By C. B. Rees .. .. — 12/–

No. 29. ——— The Decapod Larvae in the North Sea, 1950–51. By C. B. Rees
No. 30. ——— List of Records, 1953–1954. By K. M. Rae .. .. — 10/–

No. 31. The Plankton in the Irish Sea, 1951 and 1952. By D. I. Williamson 12/–

No. 32. The Hardy Plankton Indicator : A Study of the Variation between catches taken by day and by night. By R. S. Glover and J. A. Pope .. ..
No. 33. Notes on the differences between *Calanus finmarchicus* (Gunn.) and *Calanus helgolandicus* (Claus). By J. Mauchline .. .. — 6/–

No. 34. An Ecological Survey of the drift-net Herring Fishery off the North-East coast of Scotland. Part I : On Sampling by the commercial fishing fleet. By R. S. Glover, G. A. Cooper and W. W. Brown .. .. .. — 10/-

No. 35. Continuous Plankton Records: The Distribution of Young *Gadus Poutassou* (Risso). By G. T. D. Henderson, ...
No. 36. The form of *Rhizosolenia alata* Brightwell. By G. A. Robinson. .. .. — 12/-

Volume V:

No. 37. Continuous Plankton Records: The Distribution of *Calanus finmarchicus* (Gunn.) in the North Sea and north eastern Atlantic, 1946–1953. By C. B. Rees. 12/-

Printed by
Adlard & Son, Limited
at their works, Bartholomew Press, Dorking